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Modelling variation in the physiology of Bambara Groundnut (*Vigna subterranea* (L.) Verdc.)

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This thesis is submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy (PhD.)

ABSTRACT

The aim of this PhD project was to construct a model based on physiological and socio-economic factors related to the growth, development and yield of bambara groundnut landraces in relation to their environment.

The model (BamGro) is an adaptation of the PALM (Matthews, 2005) model for a leguminous crop. It is a sink-orientated model, i.e. the number of available sinks (pods) determines the final production. The model is a stand-alone computer program written in Delphi 6 (Borland®). It uses climate data, landrace specific parameters and physiological relationships and runs on a daily time-step to determine the biomass production and yield of a landrace in a specific environment. The parameters of the model have been determined with experiments in the field (Swaziland) and glasshouses (TCRU, University of Nottingham).

Large differences between glasshouse data and field data in leaf appearance rate and consequently leaf area development were found. In this study the leaf appearance rate was typically three times higher in the field, than in the glasshouse for the same landrace. When the relation between leaf area per plant and leaf number per plant is observed, there is no difference between the UK and Swaziland. The differences between the field and the glasshouse are therefore likely to be the result of an effect of environment on the leaf initiation. These differences meant that the model had to be developed with two different parameter sets, one for the landraces used in the field and one for the landraces used in the glasshouse.

BamGro is capable of describing differences between landraces, and the influence of both drought and photoperiod are simulated using a simplified approach, and these aspects can be improved when sufficient high quality data becomes available.

BamGro has been validated against three independent sets of data. BamGro achieves an excellent fit between observed and predicted data for leaf area index and pod yield, but underestimates the total above ground biomass by 50% in the TCRU glasshouses (2003 season). For the Swaziland 'Malkerns' field site (2002-2003 season) BamGro predicts the total above ground biomass excellently. BamGro achieves a good fit between observed and predicted pod yield data, but underestimates the leaf area index. For the Swaziland 'Luve' field site (2002-2003 season) the predictions are poor, with the model underestimating the total above ground biomass, leaf area index and pod yield for most landraces. BamGro is most sensitive to its crop parameters. BamGro seems not to be sensitive to changes in seasonal rainfall or initial soil moisture content.

The unavailability of data on soil water relations and incomplete agronomic data sets meant that the water routines of the model could not be validated against field data from Namibia and Botswana. Three potential uses for BamGro have been presented.

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a1	site specific Ångström coefficient
a2	site specific Ångström coefficient
Chl a/Chl b	Chlorophyll a/ Chlorophyll b ratio
DM	total drymatter (g m^{-2} d^{-1})
DM	total drymatter (g m^{-2} d^{-1})
DM_w	total drymatter (g m^{-2} d^{-1}) under water stress
e_r	efficiency of conversion of the solar radiation into biomass (g DM MJ^{-1})
e_r	radiation Use Efficiency (g MJ^{-1})
$f(\phi_d(i))$	function relating daily photoperiod to a zero-to-unity multiplier
F_{act}	actual number of flowers ($plant^{-1}$)
F_{con}	appearance constant for flowering (no. of flowers $phenochron^{-1}$)
Fpot	potential number of flowers ($plant^{-1}$)
f_{wl}	multiplier reducing the yield affected by water shortage
h	harvest index (kg DM (kg DM)$^{-1}$)
I	PAR intensity incident on the leaf (μmol CO_2 $m^{-2}s^{-1}$)
I_s	saturating irradiance
k	light extinction coefficient
k	extinction coefficient
L	Length of the leaflet (cm)
LA	leaf area (cm^2 $plant^{-1}$)
LAI	Leaf Area Index (m^2 leaf m^{-2} ground)
l_c	light compensation point for photosynthesis (μmol m^{-2} s^{-1} PAR)
LW	weight of leaves (g $plant^{-1}$)
n	recorded number of sunshine hours
n	number of days experienced by the crop since sowing
N	site specific maximum sunshine hours
$N_{flowers}$	number of flowers
N_l	total number of leaves ($plant^{-1}$)

N_l	current leaf number (plant $^{-1}$)
N_{ph}	number of accumulated phenochrons (phenochron)
N_{ph}	number of phenochrons (phenochron)
N_{pods}	pod number (pods m^{-2})
PAR	photosynthetically Active Radiation
pc	partitioning coefficient
P_{con}	weight increase constant for pods (g phenochron^{-1} (plant)$^{-1}$)
pd	plant spacing (plants m^{-2})
$P_{g, max}$	the maximum rate of photosynthesis (µmol CO_2 $m^{-2}s^{-1}$)
pi	phyllochron interval (number of leaves plant^{-1} (phenochron)$^{-1}$)
P_n	net photosynthesis rate (µmol CO_2 m^{-2} s^{-1})
PW	weight of pods (g plant^{-1})
Ra	extra-terrestrial radiation or Angot value (MJ m^{-2} d^{-1})
R_d	dark respiration (µmol CO_2 $m^{-2}s^{-1}$)
RIL	rate of increase in leaf area (cm^2 phenochron^{-1} (plant)$^{-1}$)
RIL	rate of increase in leaf area (cm^2 phenochron^{-1} (plant)$^{-1}$)
RIL_w	rate of increase in leaf area (cm^2 phenochron^{-1} (plant)$^{-1}$) - water stress
Rs	Solar radiation data (MJ m^{-2} d^{-1})
RW	weight of roots (g plant^{-1})
S	receipt of short-wave solar radiation (MJ m^{-2} d^{-1})
SLA	Specific Leaf Area (cm^2 g^{-1})
SPAD	portable chlorophyll meter (Minolta SPAD-502)
S_{total}	daily Radiation (MJ m^{-2} d^{-1})
SW	weight of stems and petioles (g plant^{-1})
T_{base}	base developmental temperature (°C)
$T_{d(i)}$	mean daily temperature (°C)
T_{high}	maximum developmental temperature (°C)
T_{opt}	optimum developmental temperature (°C)
W	Width of the leaflet (cm)
WM_1	multiplier for water stress, effecting drymatter production
WM_2	multiplier for water stress, effecting leaf area expansion
W_{pods}	pod weight (g pod^{-1})

Y	end-of season yield (kg DM ha^{-1} y^{-1})
Y_{wl}	end of season yield as affected by water shortage (kg DM ha^{-1} y^{-1})
α	the slope of the curve at low light intensity (μmol CO_2 μmol PAR)$^{-1}$
δ	0.74
$\phi_d(i)$	photoperiod (h) respectively
κ	landrace specific parameter (cm^2 $plant^{-1}$)
λ	landrace specific parameter (cm^2 $phenochron^{-1}$ $(plant)^{-1}$)
π	pi = 3.1416
ν	the proportion of flowers that will become pods
σ	leaf shape correction factor
τ	parameter to compensate for differences in leaflet dimensions
υ	parameter to compensate for inaccuracy in sample methods

CHAPTER 1 INTRODUCTION

Bambara groundnut (*Vigna subterranea* L. Verdc) is an indigenous, underutilised African legume grown primarily for its seeds, which are eaten fresh when semi ripe, as a pulse when dry and mature, or ground into a flour. It has been reported that in much of Africa, bambara groundnut is the third most important legume after groundnut (*Arachis hypogaea*) and cowpea (*Vigna unguiculata*) (Howell, 1994). Bambara groundnut has several production advantages in that it can yield on soils of low fertility and with little rainfall, it is nutritionally superior to other legumes, and is the preferred food crop of many local people (Brough and Azam-Ali, 1992; Linnemann, 1990). Despite its relative importance, bambara groundnut has not as yet received much research interest.

1.1 PROJECT BACKGROUND

In 1992, The Life Sciences and Technologies for Developing Countries Programme of the European Union agreed to fund a research project to evaluate the potential of bambara groundnut as a food crop in semi-arid Africa. The project consisted of scientific partners in three African and two European countries: the University of Nottingham, United Kingdom; Wageningen University, The Netherlands; Botswana College of Agriculture, Botswana; Sokoine University of Agriculture, Tanzania, and the University of Sierra Leone, Sierra Leone. The project objectives were (EU STD-3 Final Report, 1997) to:

1. Produce a validated model of bambara groundnut for predicting the total biomass and pod yield of different genotypes in contrasting soil and atmospheric environments (i. e. the PARCH model described in Chapter 2).
2. Identify suitable agro-ecological regions and seasons for the cultivation of bambara groundnut in Tanzania, Botswana, and Sierra Leone.
3. Identify physiological attributes associated with the ability of the crop to produce yields under semi-arid conditions.

4. Recommend suitable management practices to stabilise yields of bambara groundnut under rainfed conditions.
5. Outline a methodology for applying a similar approach to rapidly assess the potential of other underutilised species in tropical environments.

The outputs of the project are described in EU STD-3 Final Report (1997).

Following this, in 2000, the International Cooperation with Developing Countries Programme of the EU agreed to fund a second research project on bambara groundnut. Again the project had three scientific partners in Africa: the Botswana College of Agriculture, Botswana; the University of Swaziland, Swaziland and the Ministry of Agriculture, Water and Rural Development (MAWRD), Namibia. The two scientific partners in Europe were: University of Nottingham, United Kingdom and Technical University of Munich, Germany. This new project was entitled: "Increasing the productivity of bambara groundnut (*Vigna subterranea* L. Verdc.) for sustainable food production in semi-arid Africa". (BAMFOOD). The objectives of the project were to: (INCO-DC, 2001):

1. Identify bambara groundnut ideotypes for local conditions in Botswana, Namibia, and Swaziland using a farmers survey.
2. Characterise the genetic and agronomic performance of bambara groundnut landraces from Botswana, Namibia, and Swaziland in field, controlled glasshouse, and on-farm environments.
3. Evaluate genetic diversity in bambara groundnut germplasm using simple, readily transferable molecular techniques.
4. Produce a crop simulation model to help match bambara groundnut ideotypes to different contrasting environments and end users.
5. Establish an operational method of crossbreeding for intraspecific hybridisation in bambara groundnut.
6. Develop a strategic bambara groundnut breeding programme based on morphological and molecular considerations.
7. Provide a blueprint of how the methodology established for bambara groundnut can be applied to other underutilised crops.

The Institute of Water and Environment, Cranfield University, Silsoe, United Kingdom was subcontracted by the University of Nottingham to carry out the crop modelling component of the project (Item 4 above). The PhD study reported in this thesis forms part of this sub-contract.

1.2 REASONS BEHIND THIS STUDY

In contrast to major crops, which have a large literature to support research and modelling, bambara groundnut has received little research interest. Much of its literature has come from the earlier EU project, described above.

The earlier research showed large differences in the growth, production and the capability to deal with stress between landraces of bambara groundnut. However the reasons behind these differences are not always understood. Furthermore, it is not always clear which differences are most important in determining the production of bambara groundnut.

This study tries to identify the most important differences, determining the production of bambara groundnut and develop a crop growth model, capable of modelling these differences.

This model of bambara groundnut could predict the production in contrasting environments. Allthough there are already two bambara groundnut models available, these model the growth and production of bambara groundut as a species and are not capable of modelling the differences between landraces.

When varieties of bambara groundnut are being developed in the future, a robust bambara groundnut model could reduce the need for expensive field trials and assess the potential of a new variety instantaneously.

1.3 AIM AND OBJECTIVES

The aim of this PhD project was to construct a model based on physiological and socio-economic factors related to the growth, development and yield of bambara groundnut landraces in relation to their environment. Such a model could then be used to (a) match one or more existing landraces to their most suitable environments, or (b) evaluate the potential of 'theoretical' bambara groundnut ideotypes in different environments. It is important to note that this theoretical ideotype may not be available either from landraces used in the current project or within the wider bambara groundnut germplasm.

The objectives of this study were:

1. Identify the most important differences between bambara groundnut landraces.
2. Develop a suitable model framework.
3. Develop landrace specific relations to calculate development and yield in bambara groundnut and built the model.
4. Validate the model predictions against field and glasshouse data.
5. Test the model outside the environment of development.

The intention was that the model should be able to account for differences between landraces in terms of growth, development and yield, and that it would be based on a combination of results from glasshouse experiments in Europe and field experiments in sub-Saharan Africa. Gaps in data would be filled with knowledge from existing literature (much of it collected by the same project partners during the first EU bambara groundnut project) and through surveys that collated the local knowledge of growers. In addition to taking account of the constraints of the environment on growth and productivity of bambara groundnut, the specific effects of photoperiod on reproductive development and drought on yield were to be incorporated.

1.4 THESIS OUTLINE

Chapter 2 is a review of existing literature. It provides an insight into what is already known about the physiological differences between bambara groundnut landraces and gives examples of existing model frameworks. In this chapter, first the definitions of neglected and underutilised crops are given together with an explanation of why research in this area is important. After this, bambara groundnut is described in detail, followed by a short description of definitions used in crop modelling, the most important modelling approaches, some examples of existing models and the limitations of crop modelling. PARCH and BAMnut, two earlier bambara groundnut models, are described and reasons are given for why they are not used for this study.

Chapter 3 describes the materials and methods used for the development of the model. It also describes the general experimentation and is referred to, when necessary, in the subsequent chapters.

Chapter 4, a suitable modelling framework and considerations for model development used in the work are discussed.

Chapter 5 describes a preliminary experiment to determine the most important differences between three landraces. It looked at the effect of plant spacing and plant size on yield and biomass production of bambara groundnut.

Chapter 6 describes a second preliminary experiment to determine the most important differences between landraces. A detailed study investigated the photosynthetic behaviour of bambara groundnut.

Chapter 7 describes the processes of biomass production and yield formation in the model. Here a detailed description can be found of the equations used to calculate leaf appearance rate, leaf area, total above ground biomass, total below ground biomass, the appearance rate of flowers, appearance rate of pods, and the total yield.

The validation of the model is described in Chapter 8. The model has been validated against glasshouse data from the Tropical Crops Research Unit at the University of Nottingham and field data from Swaziland.

Chapter 9 presents three uses of the model outside the environment of development. It shows how the model predicts yields in Namibia and Botswana, using weather data generated with the MarkSim weather generator. The model is used to compare the performance of a theoretical ideotype and an existing landrace. Thirdly the model is used for crop forecasting.

Finally, a synthesis chapter (Chapter 10) integrates the previous chapters, investigates how the research has met the objectives and makes recommendations for future research.

1.5 DATA COLLECTION AND ANALYSIS

The candidate was directly involved in the collection and analysis of all glasshouse data at the University of Nottingham. The field data was collected by the project partners in Swaziland, Namibia and Botswana and subsequently analysed by the candidate. The candidate was solely responsible for the collection and analysis of all data of the spacing trial at the University of Swaziland (Chapter 5). The model (BamGro) is an adaptation of the PALM (Matthews, 2005) model for a leguminous crop. The candidate developed all relations/equations specific to bambara groundnut.

CHAPTER 2 BACKGROUND

2.1 NEGLECTED AND UNDERUTILISED CROPS

2.1.1 What are neglected and underutilised crops?

Neglected crops are crops that have been ignored by science and development but are still being used in those areas where they are well adapted and competitive (Hammer *et al.*, 2001). Underutilised crops are those which were formerly widely grown and consumed, but have fallen, or are falling, into disuse (Hammer *et al.*, 2001). A minor crop such as bambara groundnut falls into both categories.

2.1.2 Why are underutilised crops important?

The great advances in agricultural production of the past 50 years have resulted in a large decrease in diversity of crops and farms (Brookfield *et al*., 2002). Most of our food comes from 20 crops, nine of which are cereals (Azam-Ali *et al*., 2003). Three cereals; maize, rice, and wheat, account for about 58% of the food produced by the 20 major crops (Fowler and Mooney, 1990). Nevertheless the importance of many minor species should not be underestimated (Prescott-Allen and Prescott-Allen, 1990). Hammer (1998) estimates that there are about 100,000 species that should be considered as plant genetic resources, i.e. belonging to the gene pool of cultivated species, or having potential as prospective crop plants. Replacement of locally evolved landraces by modern scientifically-bred cultivars, however, has led to serious losses of landrace germplasm (Brookfield, 2002).

Furthermore, many crops considered neglected at a global level have a real potential to contribute to sustainable food production and food security (Hammer *et al.* 2001).

These crops are staples at a national level, provide food security during certain periods of the year, or supply the ingredients for a well balanced diet (Azam-Ali *et al.*, 2001; Hammer *et al.*, 2001).

Agricultural researchers have recently started to develop an interest in the concept of agrodiversity (Brookfield and Padoch, 1994). Brookfield and Padoch (1994) defined agrodiversity as: 'the many ways in which farmers use the natural diversity of the environment for production, including not only their choice of crops but also their management of land, water and biota as a whole'. Agrodiversity thus results from an interaction between plant genetic resources, the abiotic and biotic environments, and management practices (Almekinders *et al.*, 1995).

The concept of agrodiversity is not new. Resource-poor farmers have protected their productivity for centuries by using agrodiversity as a method to overcome spatial and temporal variations in their environment (Stocking, 2002; Brookfield, 2001).

Unlike most staples, neglected and underutilised crops, like bambara groundnut, are adapted to various marginal growing conditions (Hammer, 2001) and can be a valuable asset to an agrodiversity system.

2.1.3 Difficulties in researching underutilised crops

A major factor limiting research on underutilised and neglected crops is that germplasm is not readily accessible (Hammer *et al.*, 2001). What information on germplasm does exist is often found in the 'grey literature' (Azam-Ali, 1996) and/or documented in local languages and not readily accessible. Furthermore, because the focus of agricultural research has mainly been on major staple foods and little attention has been given to minor crops, neglected and underutilised crops have thus far failed to attract significant research funding (Azam-Ali *et al.*, 2001; Azam-Ali, 1996).

2.2 BAMBARA GROUNDNUT

2.2.1 Origin

Bambara groundnut is an indigenous African crop grown primarily for its seeds which are eaten fresh when semi ripe, as a pulse when dry and mature, or ground into a flour. The common English name appears to be derived from a tribe of agriculturalists, the Bambara, who nowadays live mainly in Mali (Linnemann, 1993). For many centuries, bambara groundnut has been cultivated in the tropical regions south of the Sahara where it is indigenous. Major producers are Nigeria, Niger, Ghana, Haute Volta, and Côte d'Ivoire, but it is also widely grown in Eastern Africa and Madagascar (Linnemann and Azam-Ali, 1993), and is even found in parts of South and Central America. The crop was taken to Asia, particularly India, Indonesia, Malaysia, Phillipines and Sri Lanka. (Linnemann and Azam-Ali, 1993), and is also found in parts of northern Australia (Linnemann, 1993).

2.2.2 Importance of bambara groundnut

In much of Africa, bambara groundnut is the third most important legume after groundnut (*Arachis hypogaea*) and cowpea (*Vigna unguiculata*) (Howell, 1994). Bambara groundnut has several production advantages in that it can yield on soils of low fertility and with little rainfall, it is nutritionally superior to other legumes, and is the preferred food crop of many local people (Brough and Azam-Ali, 1992; Linnemann, 1990). The seeds command a high market price, with demand far outweighing supply in many areas (Coudert, 1982).

Bambara groundnut is a rich source of protein. The literature reports values between 12-26% (Basu *et al.*, 2003; Essien and Akaninwor, 2000; Amarteifio and Moholo, 1998; Glew *et al*., 1997; Mnembuka and Eggum, 1995; Brough and Azam-Ali, 1992; Nwanekezi *et al*., 1994; Nwokolo, 1987; Linnemann, 1987; Aykroyd and Doughty,

1982; Poulter, 1981). In addition, Rowland (1993) reports that bambara groundnut, with its high concentration of edible protein and hence high lysine content, has a beneficial complementary effect when consumed together with cereals which generally have a low lysine content.

Recent research has established the possibility of using bambara groundnut in various food products, such as vegetable milk (Brough *et al.*, 1993), weaning food (Wambete and Mpotokwane, 2003) and 'Tempe', a traditional Indonesian food normally made by fermenting soybean with the mould *Rhizopus* (Amadi *et al.*, 1999). A preliminary study at the University of Nottingham showed that bambara groundnut can be successfully processed by extrusion, a process commonly used on an industrial scale to produce snack products among others (Lopez, 2002).

Last but not least, bambara groundnut seeds are used as feed for pigs and poultry, while the leaves and stems can be used as fodder (Doku and Karikari, 1971).

2.2.3 Morphology

Bambara groundnut is an intermediate, annual herb up to 30 cm in height with creeping, multi-branched, leafy lateral stems just above ground level (Figure 2-1). The plant has a well developed tap root with lateral roots on the lower part. In association with *Rhizobium*, the roots form rounded and some times lobed nodules (Linnemann and Azam-Ali, 1993). Bambara groundnut landraces differ in many aspects from each other, with a wide variety of seed and pod colours, and growth habits varying from bunch type, to semi bunch and spreading

Bambara groundnut has small yellow flowers. The flowers are normally carried in pairs, on short peduncles which arise from the axis formed by the petioles and the stem (Doku, 1968). The flowers produced on the same peduncle do not open on the same day, although the interval does not exceed 24 h. The flowers open in the early hours of the morning when the skies are clear. Sometimes, flower opening may be delayed due to an overcast sky or low temperature (Massawe *et al.*, 2003).

Doku (1968) reports that ants play a vital role in the pollination of the flowers, but recent research suggests that bambara groundnut is mainly self-pollinated in most environments (Massawe *et al*., 2003). In bambara groundnut, fertilisation takes place on the same day as anthesis (Linnemann, 1994). Massawe *et al.,* (2003) report that the glandular apex of the bambara groundnut flower produces a sweet secretion which attracts ants. In the natural habitat the ants loosen the soil around the glandular apex while feeding on the secretion thus assisting the penetration of the peduncle into the soil.

Figure 2-1: Bambara groundnut (*Vigna subterranea* (L.) Verdc.) 1. Habit of the flowering plant; 2, flower; 3, fruits. 4, seed. From L. J. G Maesen and S. Somaatmadja (1989)

The pods of bambara groundnut develop underground or just above the ground and may be up to 3.7 cm in diameter, depending on the landrace and number of seeds they contain. The pods are spherical or oval in shape and many contain only one seed. Pods with two seeds are also common in some landraces (Massawe *et al*., 2003). Pods with more than two seeds have also been reported (Pasquet and Fotso, 1997). Mature pods are indehiscent, ranging from yellow to reddish to dark brown or even black in colour.

2.2.4 Physiology of bambara groundnut

Germination of bambara groundnut generally takes 7 to 15 d (Kocabas *et al.*, 1999) the rate of which, when water is not limited, being dependent on temperature, genetic variability, seed size and age (Massawe *et al.*, 2002; Kocabas *et al.*, 1999; Sreeramulu, 1982). Kocabas *et al*. (1999) reported that there was no germination below 12 °C and above 45 ^{o}C, and is at a maximum at 32.9 ^{o}C. Massawe (2002) reports a similar response for germination to temperature, but notes that the response is landrace-dependent. Pre-sowing hydration has been reported to have a positive effect on the germination of bambara groundnut (Massawe, 1999), although, again the soaking time is landrace-dependent. Mabika (1992), however, reports that soaking the seeds from two bambara groundnut landraces for 24 h did not improve germination. Massawe (1999) also reports that germination is faster when in continuous darkness, indicating that germination of bambara groundnut is sensitive to the duration of light.

One of the most important factors influencing the physiology of bambara groundnut is photoperiod or daylength sensitivity. Photoperiod influences its reproductive development (Linnemann *et al.*, 1995; Linnemann and Craufurd, 1994; Linnemann, 1994; Linnemann, 1991; Nishitani *et al.* 1988) both in terms of flowering and pod formation. The degree of sensitivity, however, for both of these processes varies widely between landraces, from completely insensitive to very sensitive. Harris and Azam-Ali (1993) showed in a serial sowing study that, while there was no detectable influence of photoperiod on flowering, it did have an effect on the onset of podding. Nishitani *et al.* (1988) showed a delay in flowering of 6-11 d when plants were grown under continuous light, compared to plants grown under a normal day-and-night rhythm. Four

photoperiodic response types have been identified (Swanevelder, 1998; Linnemann, 1991):

1. Day-neutral for flowering, with a quantitative response to short days for podding
2. Day-neutral for flowering, with obligate response to short days for podding
3. Quantitative response to short days for flowering, with obligate response to short days for podding
4. Obligate response to short days for flowering

A model to quantify the influence of the effect of photoperiod on reproductive development has been developed at Wageningen University (Brink *et al.* 2000; Brink, 1999; Brink, 1997). The model was based on the photothermal approach (Summerfield *et al.* 1991; Hadley *et al.* 1984), which has been used to describe the response of flowering to temperature and photoperiod in various other leguminous crops, such as cowpea and soybean (e.g. Ellis *et al.,* 1994; Summerfield *et al.* 1993).

Leaf appearance of bambara groundnut is dependent on temperature. Massawe *et al*, (2003) report a base temperature range for leaf appearance of 8.1 to 12.0 ^{0}C depending on the landrace, and a phyllochron[1] range of 40.9 to 53.0 ^{0}C d. Both Brink (1999) and Linnemann (1994) observe that leaf production is also influenced by photoperiod. Plants grown under long photoperiods seem to produce more leaves than plants grown under short photoperiods. More research is necessary to determine if this is due to an increase in the rate of leaf production, or to an increase in the duration of the leaf production brought about by the delay in the onset of podding due to a longer photoperiod.

Bambara groundnut is widely considered to be a drought resistant crop (e.g. Collinson *et al*., 1997 and Babiker, 1989). Begemann (1988) suggests two traits that help the crop adapt to a dry environment, namely, a short growing season, and a deep root system. Collinson *et al*. (1997) suggest that drought tolerance of bambara groundnut is a result of osmotic adjustment, reduction of leaf area index, and low water loss through the

[1] the amount of thermal time between two successive leaves

stomata. Nyamudeza (1989) reported a high root to total dry matter ratio in bambara groundnut compared to other crops, while Shamudzarira (1996) found a high water use efficiency, both of which are characteristics linked to drought resistance. Also, paraheliotropism and higher leaf reflectivity have been observed when the crop is subjected to water stress (Collinson *et al.,* 1999). Mwale *et al.* (2003) report preferential allocation of dry matter to the roots with increase in the intensity of drought.

Like most other legumes, bambara groundnut has the ability to fix nitrogen through a symbiotic relationship with *Rhizobium*. Gueye and Bordeleau (1988) found in a study of 24 landraces in Senegal that 12 landraces nodulated very effectively with both indigenous and introduced *Rhizobium* strains. Most effective in this study were the indigenous strain MAO 113 and the introduced strain TAL 22. A study in Nigeria showed that nodule production rate was influenced by genotype and soil (Uguru and Ezeh, 1997). Kishinevsky *et al.* (1996) studied the nodulation and nitrogen fixation of 23 indigenous Malawian landraces grown on soil free of *Vigna subterranea*-nodulating *Rhizobia*. In this study there was no clear link between the nitrogen fixed and the pod and seed yields.

2.2.5 Agronomy & yield

Bambara groundnut is often grown as an intercrop with major commodities such as maize, millet, sorghum, cassava, yam, peanut, and cowpea (Coli, 1997; Karikari *et al.*, 1997; Ngugi, 1997) or grown in small plots as monoculture (Manthe *et al.* 2002; Ntundu, 1997). Sesay *et al.* (1999) report that almost all farmers in the study in Swaziland grow the crop as a sole crop. In Namibia, farmers assign a specific part of a field for growing bambara groundnut, and use this for many years (up to 17 years) until yields start to decline (Fleissner, 2002).

Often bambara groundnut is considered to be a ‘women’s crop’ (Manthe *et al.* 2002; Coli, 1997; Drabo *et al.*, 1997; Linnemann, 1990). For example, in Botswana, 71% of bambara groundnut fields were recorded as under female ownership (Brink *et al.,* 1996). Sesay *et al.* (1999) found that although an average of 74% of the fields were under

female ownership across all studied regions in Swaziland, there were significant differences in this proportion between regions.

One of the most time-consuming aspects of growing bambara groundnut is the practice of earthing up, also known as ridging (Manthe *et al.* 2002; Fleissner, 2002; Linnemann, 1987). This is the covering up with soil of the developing pods. Different reasons are given for this practice. For example, Sesay *et al.* (1999) cited promotion of yield, better pod development, protection of the pods against pests and protection of the pods against the sun.

Cultivating bambara groundnut is surrounded by folklore (Manthe *et al.* 2002; Sesay *et al.*, 1999; Swanevelder, 1997). Swanevelder (1997) reports, for example, that bambara groundnut cannot be planted before a maize crop has germinated, males can not walk through a bambara groundnut plot because this results in bad yields, and bambara groundnut cannot be planted in virgin soil. However, in contradiction to this, research results in Swaziland have shown that bambara groundnut can be ideally planted in virgin soil or soils that have been fallow for over two years (Sesay *et al.*, 1999).

The current yields of bambara groundnut are extremely low and variable, because the environments in which it is normally grown are characterised by various biotic and abiotic stresses (Massawe *et al.*, 2003). However, even under optimum conditions yields are variable and unpredictable due to the variability of growth and development of individual plants within a landrace (Squire *et al.* 1996).

According to Linnemann and Azam-Ali (1993) farm pod yields vary between 650 and 850 kg ha^{-1} for most of the semi-arid tropics. However there are large differences between countries, with yields as low as 56 to 112 kg ha^{-1} have been reported in Zambia, while in Zimbabwe 3870 kg ha^{-1} was obtained (Linnemann, 1987). Eyzaguirre (1997) reports values of yield in West Africa, ranging from 575 to 940 kg ha^{-1} (Table 2-1). In different studies in Southern Africa the following yields are reported: 500 to 800 kg ha^{-1} in Ghana (Doku, 1997), 50 to 660 kg ha^{-1} in Swaziland (Sesay *et al.*, 1999), and 71 to 862 kg ha^{-1} in Zimbabwe (Manyepe, 2002).

Table 2-1: Bambara groundnut yields in some West African countries (Eyzaguirre, 1997)

Country	Yield (kg ha^{-1})
Benin	643
Burkina Faso	940
Mali	672
Niger	434
Togo	575

In controlled field trials, reported yields are much higher. In Swaziland, for example, yields up to 1734 kg ha^{-1} have been reported (Sesay *et al.*, 2002), while in Namibia, Kaulihowa and Philander (2002) observed yields up to 1270 kg ha^{-1}.

2.3 CROP MODELLING

During the last three decades models have become a very important tool in agronomic research to predict the productivity of crops under varying circumstances. Besides their use in research and education, models can also be used to help make planning decisions. In this context, models are used to predict the near future.

2.3.1 Definitions

De Wit (1982) defines a model as a simplified representation of a system, and a system is a limited part of reality that contains interrelated elements. Monteith (1996) defines a crop model as a quantitative means of predicting the growth, development, and yield of a crop, given a set of genetic coefficients and relevant environmental variables. Sinclair and Seligman (1996) define crop modelling as the dynamic simulation of crop growth by numerical integration of constituent processes with the aid of computers.

A distinction can be made in the way crop models are constructed. In *mechanistic* crop models, all quantified processes have a sound physical or physiological basis (Monteith, 1996). *Empirical* models consist of functions that are chosen to fit measurements from field or laboratory (Monteith, 1996). Passioura (1996) divides crop models into two groups, depending for what purpose these are constructed. On one side are the *scientific* models, that are developed to improve our understanding of the physiology and environmental interactions of crops, and on the other side are the *engineering* models, that are developed to provide sound management advice to farmers or sound predictions to policy makers.

A model can be *dynamic*, explicitly including time as a variable and providing a means of modelling systems or variables within the system that change over the timescale of interest (Azam-Ali *et al.*, 1994) or *static*, not containing time as a variable and therefore neglecting any time-dependent aspect of the system in question (Azam-Ali *et al.*, 1994).

Most crop models currently in use are *deterministic*, they make definite predictions, there is no attempt to estimate the level of uncertainty in the predictions (Azam-Ali *et al.*, 1994). *Stochastic* models take uncertainty in input data and parameters into account.

When a model is constructed it needs to be tested against the 'real' environment in which it is going to be used. Modellers use a number of tools during the construction of their model to do just that. *Calibration* is adjusting certain model parameters or relationships to make the model output match observed data from one or more sites (Boote *et al.*, 1996). *Validation* is comparing the output of the model with a totally independent data sets (Passioura, 1996). Often modellers perform a *sensitivity analysis* on major inputs and parameters (Monteith, 1996), in order to evaluate the response of the model to these inputs and parameters.

2.3.2 Examples of models

Most crop models combine calculations, based on physiological data, with empirical relations to predict the production of a plant or crop (Boote *et al.*, 1996). The outcome of these models is a clear prediction of production (e.g. yield), and can easily be used in decision-making. Many models have been developed for many different crops. Some examples are mentioned in Table 2-2.

Table 2-2: Examples of crop models

Crop	Model	Reference
Maize	CERES-Maize	Jones and Kiniry, 1986
Groundnut	PNUTGRO	Boote *et al*., 1989
Soybean	SOYGRO	Wilkerson *et al*., 1985
Faba bean	CROPGRO-Faba bean	Boote *et al*., 2002
Tomato	CROPGRO-Tomato	Scholberg *et al*., 1997
Tea	CUPPA-TEA	Matthews and Stephens, 1998a and 1998b
Chickpea	CHIKPGRO	Singh and Virmani, 1996
Cassava	GUMCAS	Matthews, 1994
Wheat	Sirius	Jamieson *et al*.; 1998
	WTGROWS	Aggarwal *et al*., 1994
	SWHEAT	Van Keulen and Seligman, 1987
	CERES-Wheat	Ritchie *et al*.; 1985
	AFRCWHEAT	Weir *et al*., 1984

2.3.3 Complex versus simple models?

As early as 1973, Passioura pointed out the dangers in using complex mechanistic simulation models because of the difficulties inherent in testing them and the wide gap between crop growth and yield and molecular processes (Passioura, 1973). On the other hand simple models may not be sufficiently realistic to allow testing of some hypotheses or sufficiently robust for meaningful application (Savin *et al*., 1994).

The level of complexity needed for a specific model depends on the objectives and questions being asked of the model. It also depends on the amount of data and time available for model building and testing (Boote *et al*.; 1996). A more complex model does not automatically mean a better model. Complex models require more parameters than simple models. Experimental error while determining these parameters leads to cumulative errors in the model (Passioura, 1996; Sinclair and Seligman, 1996; Aggarwal, 1995). Some parameters that cannot be measured have to be estimated, or

even ‘guestimated’ (Sinclair and Seligman, 1996) resulting in more uncertainty in the model. When calibrating the parameters against observed data, there is a danger that the exercise turns into mere ‘curvefitting’ (Sinclair and Seligman, 1996; de Wit, 1970).

Soltani *et al*. (1999) argue that, because complex models include a large number of assumptions and parameters and require large amounts of information about the soil and crop system, the complexities in specifying the inputs and in interpreting how the model works make it difficult to use.

2.3.4 Limitations of crop models

A common problem with crop models is their often limited validity. Some models are developed for a certain environment and may not be valid when used in a different environment (Passioura, 1996; Monteith, 1996).

Soil and weather inputs required by the crop models show spatial and temporal variation and may have considerable measurement errors (Aggarwal, 1995) resulting in further uncertainties in the outputs of crop models.

Most crop models are built combining proven relations that have been tested over a range of environments, new relations that have only be tested in the environment in which they were developed and hypotheses that have not been tested at all. It is difficult to test the crop model as a whole, without measurements that describe the performance of the crop over a wide range of environments (Monteith, 1996). This makes many crop models difficult to validate.

A good example of models that have overcome these limitations by thorough validation in many different environments and are now considered to be ‘fairly’ universal are the DSSAT (Decision Support System for Agrotechnology Transfer) models (Uehara and Tsuji, 1993). These models were a product of the International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT). The DSSAT software package consisted of (Matthews *et al*., 2000):

1) A database management system to store and retrieve the minimum dataset of soil, crop, weather and management data to validate and apply the crop simulation models.
2) A set of validated crop models to simulate the outcomes of genotype x environment x management interactions.
3) Application programs that facilitate the manipulation of databases, the use of crop models, and the presentation and analysis of the model output.

2.3.5 Use of crop models

Crop growth models are used increasingly for estimating production potentials (e.g. Azam-Ali, *et al*., 2001, Matthews, 1998a; Matthews, 1998b; Aggarwal and Kalra, 1994), management (e.g. Matthews, 2002a; Aggarwal and Kalra, 1994, Angus *et al*., 1993), education (e.g.Graves *et al*., 2002), decision support systems (e.g. Stephens and Middleton, 2002; Lee *et al*. 1995), crop genotype improvement (e.g. Stewart, 2003; Matthews, 2002b), defining research priorities (e.g. Matthews, 2002c), technology transfer (e.g. Matthews *et al*.,2000) and predicting the effects of climatic change (e.g. Matthews *et al*. 1997; Matthews *et al*.1995; Adams *et al*., 1990).

Since the 1970s an enormous boom in model development has taken place. At the beginning of this boom, the mere development of a comprehensive model was an innovation and an extension of the discipline of crop science (Sinclair and Seligman, 2000). Concern starts to grow about the continuing growing number of models. Mathematical representations for most of the major crop processes have now been developed (Matthews and Stephens, 2002). There might still be some scope for refinement of these processes, but it is unlikely that this improves the accuracy and reliability of the models at the crop level (Matthews and Stephens, 2002). New models or adaptations/improvements of existing models can still be developed for crops that have a limited research history, like bambara groundnut.

Sinclair and Seligman (2000) recognised the abovementioned situation. Although they do acknowledge the fact that many new models have a local practical interest, these

models may not always present an analysis of general scientific interest. Sinclair and Seligman (2000) suggest three criteria that should be met in a crop modelling paper to make it suitable for scientific publication:

1) A clear statement of a scientific objective with a defined domain of relevance
2) A mechanistic framework
3) An evaluation of the scientific innovation offered in the new model.

When modelling is looked at from a strictly scientific point of view Sinclair and Seligman (2000) are right with their criteria. However many models which have a local practical interest open the door to a deeper scientific understanding of the context for which the model is used. An example of the use of a model to provide new insights into crop processes for future research is reported by Matthews and Stephens (1998b). During the development of a simulation model for tea (*Camellia sinensis*), it was found that temperature alone could not be used to simulate the large peak in tea production in September in Tanzania. This finding led to new hypotheses and a better understanding of the development of the crop.

2.4 REVIEW OF EXISTING MODELS OF BAMBARA GROUNDNUT

Two earlier models of bambara groundnut have been developed at the University of Nottingham.

2.4.1 PARCH based model (Collinson, 1996; EU STD-3 Final Report, 1997)

The first model is based on the PARCH (Predicting Arable Resource Capture in Hostile environments) model developed at the University of Nottingham, initially for sorghum (Bradley and Crout, 1993). PARCH incorporates a crop growth module, coupled with a soil profile divided into layers (Figure 2-2).

The initial development of the model was based on an experiment conducted in 1990 at the Tropical Crops Research Unit (TCRU) at the University of Nottingham (Kenyi, 1991; Collinson *et al.* 1996).

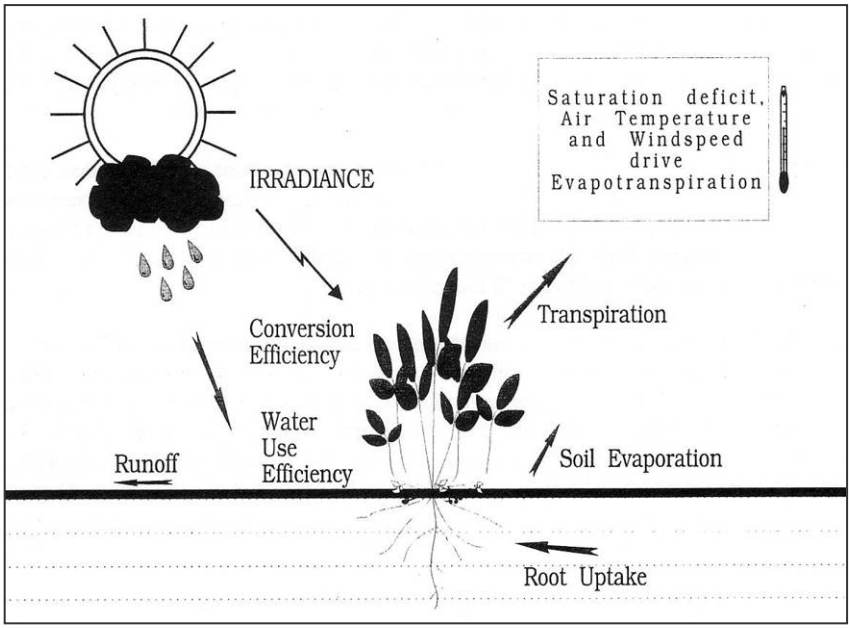

Figure 2-2: Pictorial overview of the PARCH model (EU STD-3 Final Report, 1997)

The model works on a daily timestep. Each day, water and light are captured and converted into dry matter. Growth is initially partitioned to stems, leaves and roots, according to landrace specific parameters (Table 2-3) until podding starts. When podding has been achieved, drymatter is preferentially directed to the pods.

Table 2-3: Model parameters for three bambara groundnut landraces (Collinson, 1996)

Parameter	DodR	DipC	LunT
Conversion coefficient (g MJ^{-1})	1.1	1.1	0.85
Transpiration equivalent (g kPa kg^{-1})	4.2	4.6	4.3
Extinction coefficient	0.5	0.5	0.7
Initial fraction below ground	0.3	0.34	0.2
Initial fraction to leaf	0.75	0.72	0.75
Initial fraction to stem	0.25	0.28	0.25

Growth is dependent on either light or water, whichever is most limiting on a given day. The plant becomes stressed when the supply of water from the soil/root system is not sufficient to maintain the potential transpiration rate. The potential transpiration rate is determined by light driven growth. Water stress causes increased partitioning of assimilates to the roots at the expense of pod yield, in an attempt to increase water uptake.

The model was calibrated using controlled environment data from a 1995 glasshouse experiment at the University of Nottingham for one landrace grown under irrigated and droughted conditions (Collinson, 1996).

The model was then validated against field data from Sierra Leone and Tanzania. Where solar radiation data was not available, the model calculated solar radiation from sunshine hours, using the Ångström equation (Ångström, 1924).

2.4.2 BAMnut (Bannayan, 2001; Azam-Ali *et al.*, 2001)

BAMnut was an improvement of the original PARCH-based model. The model was designed with functional relations derived from glasshouse and growth room experiments at the University of Nottingham (Kocabas *et al.*, 1999; Collinson *et al.*, 1999; Collinson *et al.*, 1997 Berchie, 1996; Zulu, 1989; Babiker, 1989) and field experiments conducted in Africa (Sesay and Yarmah, 1996; Karikari *et al.*, 1996). The objective of the model was to predict crop performance of bambara groundnut under both optimal and water limited conditions.

BAMnut simulates dry matter production and pod yield through numerical integration over a daily timestep. Depending on the availability of the resources light and water, the production is either light limited or water limited (see Figure 2-3). Light limited growth (LLG) is calculated from incoming solar radiation and the fraction of this solar radiation intercepted by green leaves. Water limited growth (WLG) is calculated from potential water uptake rates and the amount of available water in the rooting zone. LLG and WLG are then compared, and actual growth taken as the minimum of the two. Pod yield

is determined at crop maturity as the product of accumulated above-ground dry matter and a constant landrace specific harvest index (Azam-Ali *et al.*, 2001).

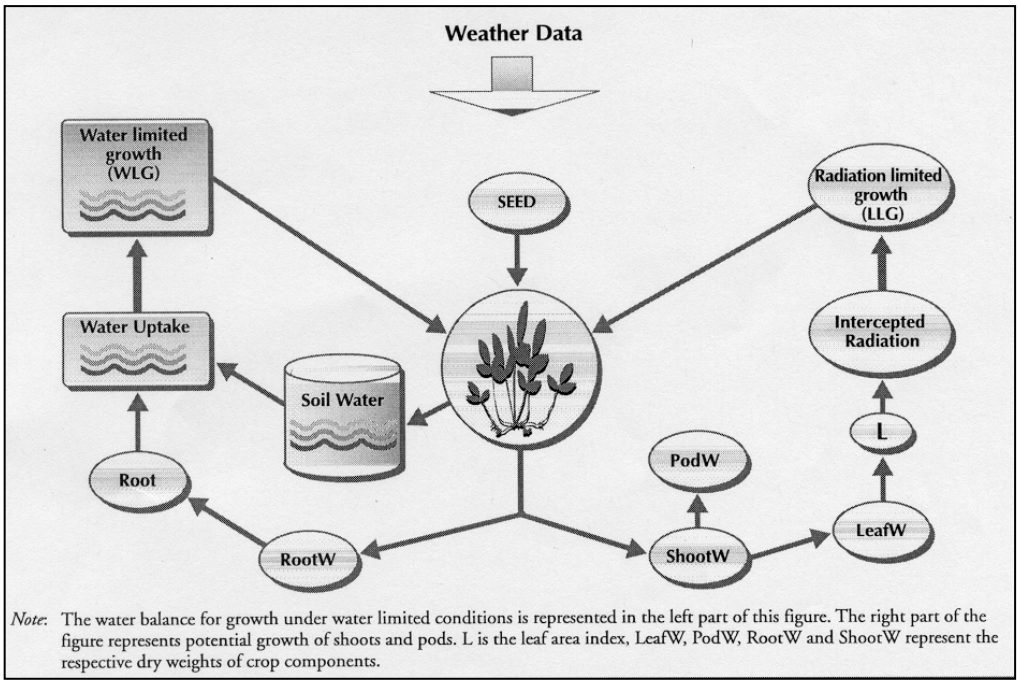

Figure 2-3: Relational diagram of the BAMnut model (Azam-Ali *et al.*, 2001)

BAMnut needs daily weather data as an input. The minimum inputs for BAMnut are solar radiation, minimum and maximum temperatures, and rainfall. BAMnut used an adapted weather generator (Matthews and Stephens, 1996) to generate these inputs from a world climate data base.

BAMnut and the weather generator are both integrated into a Geographical Information System (GIS), to give outputs consisting of maps and statistics of suitable areas in the world for bambara groundnut production. Predicted biomass and pod yield from multiple simulations were classified into four representative ranges of suitability (Table 2-4), based on reported good yields of bambara groundnut in different regions of Africa.

Table 2-4: Classification of suitability ranges for predicted biomass and pod yield of bambara groundnut (Azam-Ali *et al.*, 2001)

	Very Suitable	Suitable	Moderately Suitable	Unsuitable
Biomass (kg ha^{-1})	>8,500	4,500-8,500	1,500-4,499	<1,500
Pod yield (kg ha^{-1})	>3,000	1,000-3,000	300-999	<300

2.4.3 Why a new bambara groundnut model?

The PARCH based model (Collinson, 1996) was a preliminary attempt to evaluate the agro-ecological potential of bambara groundnut as a species. The model was based on very limited data from the first EU project, much of which came from controlled environment experiments. The BAMnut model (Bannayan, 2001; Azam-Ali *et al.*, 2001) used the original PARCH model and applied it in a mapping projection for potential global distribution of bambara groundnut.

Both models were using well established principles of resource capture from other crops. Parameters for bambara groundnut were established for these mostly empirical relations. The approach for the new model was to base it as much as possible on the actual relations governing development and production in bambara ground nut that can be tested in field or controlled environment experiments.

The PARCH and BAMnut models were source oriented models, i.e. the ability to capture and convert resources (light and water) determines the final production. An attempt was made to model differences between landraces by determining landrace specific parameters for resource capture, but this was unsuccessful.

Two preliminary experiments in this study (Chapter 5 & 6) showed that landraces differ more in the number of available sinks (pods) than in their ability to capture and convert resources, indicating that a sink orientated approach would be more appropriate.

It is well known that photoperiod sensitivity ranges in landraces from photoperiod insensitive to sensitive for both flowering and pod formation (Linnemann, 1991), yet neither of the two models has an approach to simulate the effect of photoperiod. As the effect of photoperiod is a very important factor determining the final production of bambara groundnut in a given environment the new model should have an approach to simulate the effect of photoperiod.

These limitations of the models and the unavailability of the original model code from both the PARCH and BAMnut model led to the decision to base the new model (BamGro) on the PALM (Matthews, 2005) model for a leguminous crop. The PALM model was sink orientated and had a well tested robust structure that was easily adapted to model bambara groundnut. A simplified overview of the structure of the new BamGro model can be seen in Figure 2-4.

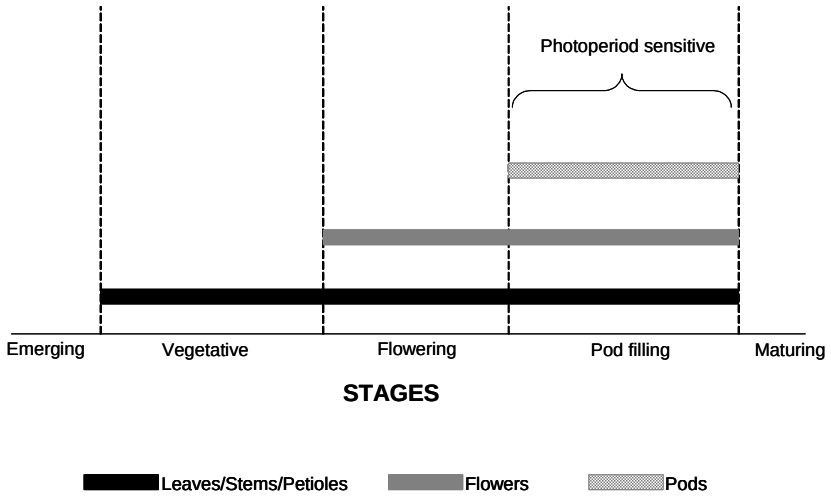

Figure 2-4 Simplified structure of the BamGro model

CHAPTER 3 MODEL DEVELOPMENT: MATERIALS AND METHODS/ MODEL INPUTS

Three types of experiments were conducted to develop the equations used in the model, calibrate and validate the model, and test its predictions. Data collected in glasshouse experiments were used to determine growth, development and photosynthetic behaviour of bambara groundnut *stands* under controlled conditions where soil moisture was varied, whilst other factors such as solar radiation, air temperature, daylength, and atmospheric saturation deficit were common. A pot experiment was used to determine the photosynthetic behaviour of bambara groundnut *plants* under droughted and unlimited soil moisture conditions. Field experiments were used to determine growth and development of rainfed bambara groundnut *crops* under natural radiation and daylength. The experiments in Swaziland were used to develop the model equations, while the experiments in Botswana and Namibia were used to calibrate and test the model.

3.1 CHOSEN LANDRACES

Landraces are crop populations that have not been bred as cultivars but have been adapted through years of natural and artificial selection to the conditions under which they are cultivated.

All landraces used in this project (Table 3-1) were either collected from farmer's fields or bought from local markets. Allthough the Namibian and Botswanan landraces went through a more rigorous selection than the Swaziland landraces, which were grouped on seed colour and eye pattern only, none of the landraces has been bred as a cultivar.

The landraces were chosen to represent a wide range in seed colours, seed patterns and agronomic characteristics. S19-3, a black landrace, was added to the glasshouse

experiments at the University of Nottingham. This landrace was very early maturing and had a very rigorous growth.

Table 3-1: Landraces used by all partners. The landraces from Swaziland and Namibia have not been characterised (choice based on eye colour) and have not been previously used in experiments. The Botswana landraces have been characterised and two (DipC and GabC) were used in the previous EU funded project.

Origin	Landrace	Source	Description
Swaziland	NyakeniC1	Farmer at Nyakeni	Cream testa, black eye pattern
	NyakeniC2	Farmer at Nyakeni	Cream testa, brown eye
	UniswaRed	Manzini market	Red testa, white helium
Namibia	AHM753	Namibia germplasm	Red testa, early maturing
	AHM968	Namibia germplasm	Tan colour, medium maturing
	AS17	South Africa	Late maturing
Botswana	DipC	BCA germplasm	Cream testa, black eye
	GabC	BCA germplasm	Cream testa, brown eye
	OM1	BCA germplasm	Cream colour, butterfly eye

3.2 GLASSHOUSE EXPERIMENTS AT THE UNIVERSITY OF NOTTINGHAM

3.2.1 Tropical Crops Research Unit (TCRU) Glasshouse System

There are five TCRU controlled-environment glasshouses. The houses are aligned north to south, and are spaced 15 m apart to prevent mutual shading. Each house has a cropping area of 35 m^2 containing a sandy loam soil (bulk density 1.3 g cm^{-3}) overlying a gravely loam subsoil (Collinson *et al*., 1996).

The original design and control system of the TCRU glasshouses were described by Monteith *et al.* (1983) and and improvements and alterations implemented in 1990 were reported by Clifford et *al.* (1993).

The soil within each is isolated from that external to the glasshouse by a heavy-duty butyl liner installed to a depth of 1.25 m to prevent influences of the natural movement of the groundwater table. A similar lining subdivides each house into two plots, each approximately 16 m^2 in area. In these experiments, each glasshouse had an irrigated and a dry treatment.

The temperature in the glasshouses was maintained at 27 °C with a sinusoidal diurnal variation of ± 5°C amplitude. Heat was supplied via gas-fired heaters (Powrmatic Ltd, UK), with an atmospheric flue to vent the fumes to the outside of the glasshouse. Saturation deficit was not controlled during the course of this experiment.

The soil in each plot was sterilized with methyl bromide two weeks prior to sowing, then hand cultivated and rake harrowed to create a fine tilth seedbed.

3.2.2 Main experiment (2000, 2001, 2002, 2003)

Three bambara groundnut landraces, S19-3 (Namibia), DipC (Botswana) and UniswaRed (Swaziland) were sown directly into the soil of three TCRU controlled environment glasshouses (Table 3-2) at the Sutton Bonington Campus of the University of Nottingham. In the 2000 preliminary season, five landraces were sown, DodR (Tanzania) and LunT (Sierra Leone) were added to three mentioned above.

Table 3-2: Sowing dates of the main experiments

Year	Sowing date
2000	14 June 2000
2001	31 May 2001
2002	17 May 2002
2003	28 April 2003

In each experiment, seeds were sown at 5 cm depth and at 10 cm intervals in rows spaced 30 cm apart. After 21 days, thinning took place to 20 cm intervals within the rows, leaving an average planting density of 16.7 plants m^{-2}.
Soil moisture was determined weekly by neutron probe (Didcot Instruments, Wallingford, UK) and profile probe (Delta-T Devices). Both treatments were irrigated weekly to field capacity until 50% flowering was reached. After this time, the dry treatment received no further irrigation, while the wet treatment was irrigated up to field capacity weekly (In the 2001 experiment determination of the moisture content of the soil could not be done, both plots received 20 mm of water weekly until 50% flowering was reached after this the wet plot received 20 mm of water weekly, while the dry plot was left without irrigation). Irrigation was applied by PVC microporous tubing placed between the rows, and the amount of water applied to each plot measured using a programmable water meter.

The crop received natural daylight with no supplementary lighting. Daylength was controlled at 12 h d^{-1} by covering the crop with a black polythene screen fitted over a metal frame above the crop. The amount of light intercepted was measured using three tube solarimeters within each plot. Incoming radiation was measured by one solarimeter located above the plot, while the radiation below the crop stand was measured with the remaining two solarimeters located on the soil surface across the rows within the central 2 m^2 of the plot. Readings were recorded every 30 seconds on a datalogger (Campbell Scientific CR10) and averaged for every hour.

Phytoseilus persimilis was used as a biological pest control against red spider mite (*Tetranycus urticae*) every two weeks.

3.2.3 Pot experiment (2001)

The pot experiment was conducted in a faculty glasshouse bay with a concrete floor at the University of Nottingham Sutton Bonington campus. Three bambara groundnut landraces, S19-3 (Namibia), DipC (Botswana) and UniswaRed (Swaziland) were used

for this experiment. Three seeds were sown per pot (∅ 23 cm) on 30 May 2001, and after establishment, seedlings were removed to leave one healthy seedling remaining. In total, ten plants of each landrace remained. The temperature in the glasshouse was maintained at a daily mean of 32°C (with a ± 5°C diurnal variation). The plants were watered twice a week, with water being applied until drainage from the bottom of the soil profile occurred to ensure a maximum amount of available water and reduce the risk of creating heterogeneity between the pots.

No nutrients were added to the medium, as it was assumed that those provided by the compost (John Innes, no. 3) were sufficient.

The plants grew under natural light, supplemented with artificial light (400 W high pressure sodium - Son T Supplementary) between 6 am and 6 pm for the duration of the experiment, to make up for the light loss caused by the structure of the glasshouse bay. Daylength was not controlled. The plants were sown on 30 May 2001 and the last measurements were done on 16 August, resulting in a photoperiod of between 15 and 17 h during the experiment.

Biological pest control (*Phytoseiulus persimilis*) against red spider mite was applied every two weeks after the first signs of infection (21 days after sowing). At 70 DAS, the plants were sprayed with a chemical (Torque – Fenbutatin Oxide) to control a late infestation.

3.3 ROUTINE MEASUREMENTS IN THE GLASSHOUSE

3.3.1 Main experiment (2000, 2001, 2002, 2003)

3.3.1.1 Emergence

The number of emerged seedlings was recorded in all plots up until 21 DAS. A seedling was defined as having emerged when the first true leaf was visible.

3.3.1.2 Leaf counts

Leaf counts were carried out twice a week for the duration of the experiment on 10 selected/pre-determined plants, which were tagged after emergence. At the end of the experiments, the plants were harvested and used for a normal growth analysis.

3.3.1.3 Growth-analysis

Every 21 days, starting 21 DAS, a growth analysis was conducted. Ten plants were selected at random and harvested. From these plants, the number of leaves, pods and flowers were determined, and the leaf area measured with a leaf-area meter (LI-COR 3000). The sampled plants were then dried at 80 $^{\circ}$C for 48 h and the dry-weights of leaves, stem/petioles and pods were measured.

At the end of the experiment, ten plants were selected from the central area of the plot (approximately 2 m^2), until then untouched, and these were used for normal growth analysis and determination of final yield.

3.3.2 Pot experiment (2001)

3.3.2.1 Leaf counts

Leaf counts were carried out twice a week on all plants.

3.3.2.2 Final growth analysis

At the end of the experiment the plants were harvested. From these plants, the number of leaves, leaf-area and flowers were determined. After this the plants were dried at 80 ^{o}C for 48 h and the dry-weights of leaves and stem/petioles were measured.

3.4 FIELD EXPERIMENTS (SWAZILAND, BOTSWANA, NAMIBIA)

Nine bambara groundnut landraces, three from each African partner (Table 3-1), were planted at two sites in each country, namely Notwane and Good Hope in Botswana; Mahanene, and Mashare in Namibia, and Malkerns and Luve in Swaziland (Figure 3-1).

The sites were chosen for their differences in temperature and rainfall, and can be seen as representative for different agro-ecological zones in Southern Africa (Figure 3-1, Table **3-3**).

Table 3-3: Geographical location, altitude and annual rainfall of the field sites in Botswana, Namibia and Swaziland.

		Lattitude	**Longitude**	**Altitude (m above sea level)**	**Annual rainfall (mm)**
Botswana	**Notwane**	24º33' S	25º54' E	994	400-600
	Goodhope	25º28' S	25º26' E	1245	300-400
Namibia	**Mahanene**	17º27' S	14º45' E	1110	400
	Mashare	17º48' S	20º41' E	1060	>500
Swaziland	**Malkerns**	26º30' S	31º13' E	700	850-1000
	Luve	26º20' S	31º14' E	580	700-850

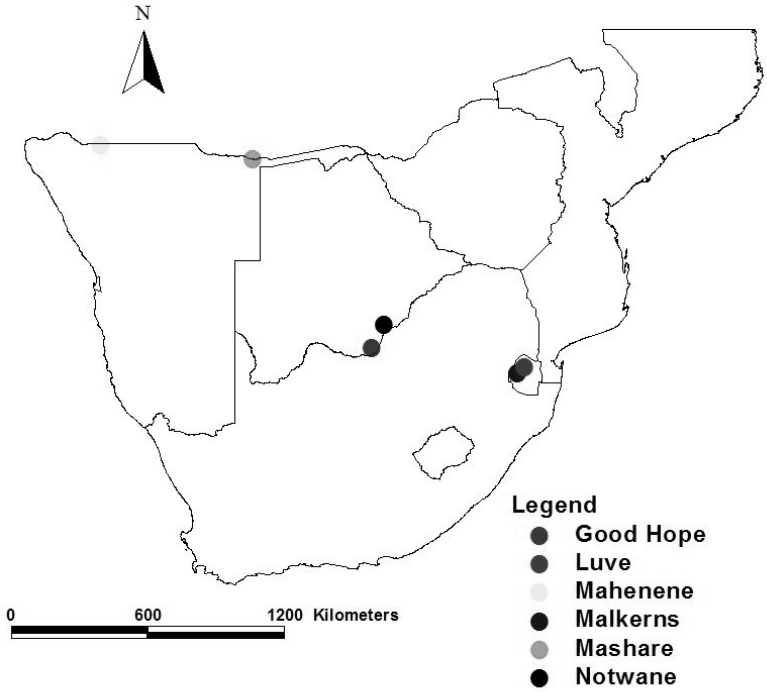

Figure 3-1: Location of field sites in Namibia, Botswana and Swaziland

The experiments at each field site comprised of four replicate blocks of nine plots (landraces) giving a total of 36 plots. Each individual plot was 6 x 6 m, i.e. 36 m^2. The inter- and intra-row spacing was 50 and 30 cm, respectively, giving a plant population of 7 plants m^{-2} (252 plants per plot). Two seeds were sown per hill (Table 3-4) and half intra-row spacing at a depth of 5 cm, and thinned down to one per hill and appropriate spacing 21 days after sowing.

Table 3-4: Sowing dates for three seasons at field sites in Botswana, Namibia and Swaziland.

		2000-2001	2001-2002	2002-2003
Botswana	**Notwane**	13 December	27 November	18 December
	Goodhope	12 December	20 November	12 December
Namibia	**Mahanene**	2 February	30 January	8 January
	Mashare	30 January	30 January	31 December
Swaziland	**Malkerns**	16 November	22 November	25 November
	Luve	6 December	8 January	9 January

The experimental area was tractor ploughed and harrowed after which plots were hand cultivated with hoes and raked to a good tilth before planting. All plots were fertilized (broadcast) with NPK compound fertilizer (2-3-2) at the rate of 500 kg ha^{-1} and incorporated into the soil at planting. In 2000 the experimental area was limed with calcium carbonate, at the rate of 2 t ha^{-1} three weeks before planting. In all experiments the seed was dusted with the fungicide Captab *(cis-N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide)* at 12 g 10 kg^{-1} seed, according to the manufacturer's directions. Cutworm bait (KOMBAT – Sodium Fluosilicate) was applied along the rows at emergence. In 2000 plants were sprayed with the insecticide Malathion (50% EC) and the fungicide Benlate, as necessary, to control aphids and diseases, respectively, using a knapsack sprayer. Benlate was sprayed weekly during the reproductive period to limit the loss of plants through secondary infections associated with a serious root-knot nematode (*Meloidogyne* spp) infestation. In the 2001 and 2002 crop seasons a nematicide (Nemacur 10 GR, Bayer AG) was applied at both experimental sites, to prevent the plant mortality experienced at Luve during the previous season due to root-knot nematode infestation. The nematicide was applied at a rate of 1.5 g m^{-1} of row, before planting, and a regular schedule (bi-weekly) of prophylactic spraying of insecticide (Malathion) and fungicide (Eria 187,5 SC Novartis South Africa; difenoconazole (triazole) and carbendazim) was followed throughout the growing season. In all three crop seasons plots were weeded by hand, and earthing up was done after 100% flowering. The crop was rain-fed and no supplementary irrigation was given.

3.5 ROUTINE MEASUREMENTS IN THE FIELD

3.5.1 Emergence

The number of emerged seedlings was recorded in two rows per plot until 21 DAS. A seedling was defined as having emerged when the first true leaf was visible.

3.5.2 Leaf counts

Leaf counts were carried out twice a week for the duration of the experiment on 10 selected/pre-determined plants, which were tagged after emergence.

3.5.3 Flowering

Flower counts were carried out on 10 selected/pre-determined plants, which were tagged after emergence. Flowers were counted twice weekly for the duration of the experiment.

3.5.4 Growth analysis

Eight plants were selected per plot for sequential growth analysis. From these plants, the number of leaves, pods and flowers were determined. The plants were then dried at 80 ^{o}C for 48 h and the dry-weights of leaves, stem/petioles and pods were measured. Growth analysis started at 21 DAS and subsequently at 14 days intervals, i.e. 35, 49, 63, 77, 91, 105 and 119 DAS.

3.5.5 Final harvest

Ten plants per plot were sampled for final harvest measurements. At harvest the number of leaves per plant and total dry weights were determined for ten individual plants per plot. The final number of pods was determined. Seed weight was determined at oven dry weight and converted to 10% moisture.

3.5.6 Leaf area

In the field experiments, leaf area per plant could not be measured with a leaf area meter. Therefore, leaf area was estimated at Malkerns and Luve during the 2001-2002 season from measurements of leaf width and length, using a method based on the following assumptions (Cornelissen *et al,* 2002; Deswarte, 2001):

- The bambara groundnut has leaves with a shape very close to an ellipse (Figure 3-2):

Area for the ellipse: $A = L * W * \pi /4$ (1)

Equation to estimate the leaflet area: $A = \sigma * L * W * \pi /4$ (2)

Where: L = Length of the leaflet (cm)

W = Width of the leaflet (cm)

$\pi = 3.1416$

σ = correction factor (to account for the difference between the actual shape and an ellipse)

- The size of the lateral leaflets are usually closely related to the size of the middle leaflet
- The plant leaf-area is a function of the leaf number and the single-leaf area.

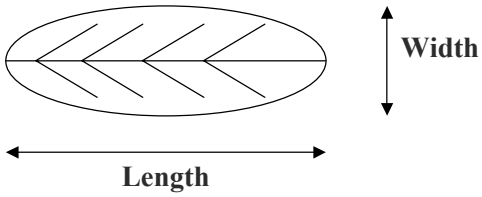

Figure 3-2: Length and width measurements of a bambara groundnut leaflet

Bambara groundnut has trifoliate leaves; although these three leaflets have the same shape, they do not always have the same dimensions or leaf area. In order to compensate for these differences an extra parameter τ is added to Equation 2:

$$A = \tau * 3 (\sigma L * W * \pi /4) \quad (3)$$

The step to leaf area of the whole plant seems to be simply multiplying Equation 3 with the total number of leaves (N_l), however an extra parameter (υ) needs to be added to compensate for inaccuracy in sample methods. Young not fully unfolded leaves and leaves that look significantly smaller than others are rejected. This can lead to under or overestimation of the leaf area. The equation becomes:

$$A_{plant} = \upsilon * N_l [\tau * 3 (\sigma * Length * Width * \pi /4)] \quad (4)$$

Deswarte (2001) calculated landrace independent values for σ, τ and υ, given in Table 3-5 and the relation between actual and estimated leaf area is shown in Figure 3-3.

Table 3-5: Landrace independent values for calculating bambara groundnut leaf area

Model Parameters	Landrace independent values
σ	0.95
τ	0.91
υ	0.86
R^2	90.90%

For practical purposes, equation 4 can be simplified by subsuming σ, τ and υ into δ (δ=0.74):

$$A_{plant} = 0.74 * 3 * N_l (Length * W * \pi /4) \quad (5)$$

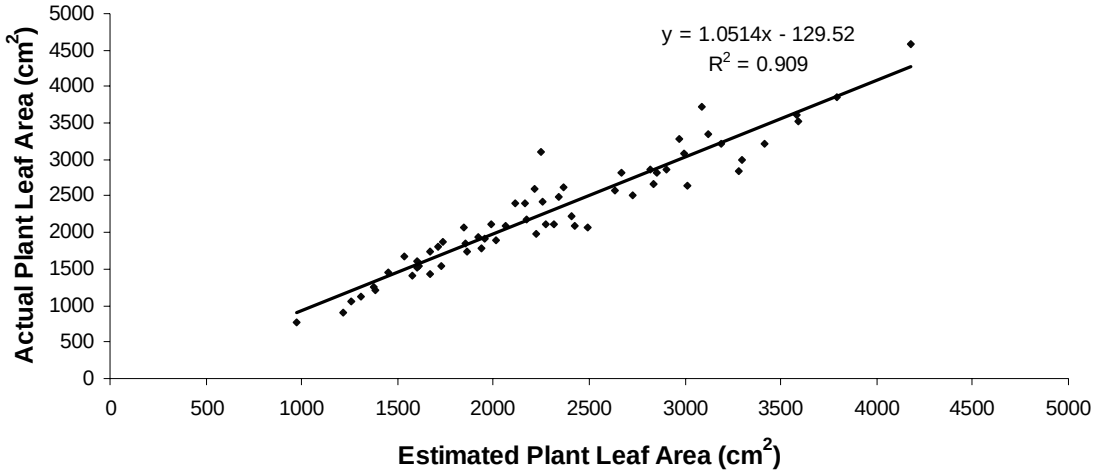

Figure 3-3: Relation between estimated plant leaf area and actual plant leaf area (Deswarte, 2001)

CHAPTER 4 MODEL DEVELOPMENT: CONCEPTUAL FRAMEWORK

4.1 STARTING FRAMEWORK

Crop yields are considered as (a) potential (i.e. limited only by temperature, solar radiation, photoperiod, CO_2 level and genotype (in the case of bambara groundnut, landrace) characteristics), and (b) water-limited, i.e. as for (a), but with water availability also taken into account (Monteith, 1994). The summary framework is the following:

$$Y = Se_r\left(1 - e^{-kLAI}\right)h$$

where Y is the end-of season yield (kg DM ha^{-1} y^{-1}), S is the receipt of short-wave solar radiation (MJ m^{-2} d^{-1}) over the growing period, e_r is the efficiency of conversion of this solar radiation into biomass (g DM MJ^{-1}), k is the light extinction coefficient, LAI is the average leaf area index (m^2 leaf m^{-2} ground) over the growing season, and h is the harvest index (kg DM (kg DM)$^{-1}$).

Breaking up this equation in its separate components gives an indication of the most important factor determining the yield. The receipt of solar radiation (i.e. irradiance above the plants, S) cannot be influenced and will be the same for all plants in the field. More important is the Radiation Use Efficiency, e_r. Mwale (2005) reported an e_r of 2.75 g DM MJ^{-1} based on Photosynthetically Active Radiation for the landraces used in this study and finds no real significant effect of landrace for the 2000 and 2001 season in the TCRU glasshouses at the University of Nottingham (main experiment, described in Chapter 3). These values are in agreement with those in the literature (Collinson *et al*., 1996) [ranges between 1.0 and 2.8 g DM MJ^{-1} based on Photosynthetically Active Radiation]. The light extinction coefficient is influenced by the shape of the canopy. As all the landraces used in these experiments have a similar shape, it can be assumed k

will be similar for the different landraces. Although landraces differ in their rate of leaf area development, all landraces reach a leaf area index of 3 after 60 DAS (Figure 4-1). Using a common k value of 0.6, i.e. canopies with relatively lax leaves, all landraces are assumed to reach 80% light interception after 60 days.

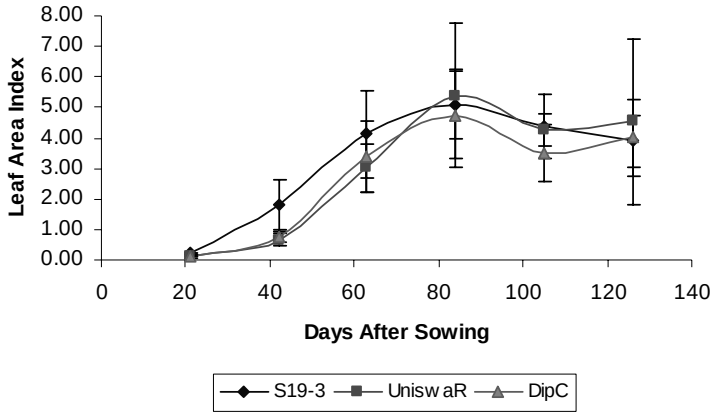

Figure 4-1: Change in Leaf Area Index in time for the 2001 glasshouse season at the TCRU, University of Nottingham, average of 10 plants, error bars are standard error of the mean.

From the experiments, it was found that the Harvest Index was significantly different between landraces and treatments (Table 4-1). Furthermore the correlation between Harvest Index and yield was weak, pointing to high variability within the landrace (Figure 4-2).

Table 4-1: Average Harvest Index* (%) ± standard error of the mean (2000: average of 40 plants; 2001: average of 10 plants) for five landraces grown in controlled environment experiment at TCRU, University of Nottingham.

	Irrigated		Dry	
Lanrace	2000	2001	2000	2001
Uniswa Red	41 ± 10	26 ± 9	31 ± 18	38 ± 11
DipC	48 ± 7	49 ± 7	38 ± 12	46 ± 3
S19-3	54 ± 5	49 ± 6	55 ± 6	48 ± 5
DodR1999	47 ± 10	No data	46 ± 16	No data
LunT1999	29 ± 15	No data	18 ± 11	No data

*The harvest index represents the pod yield as proportion of the total above ground biomass.

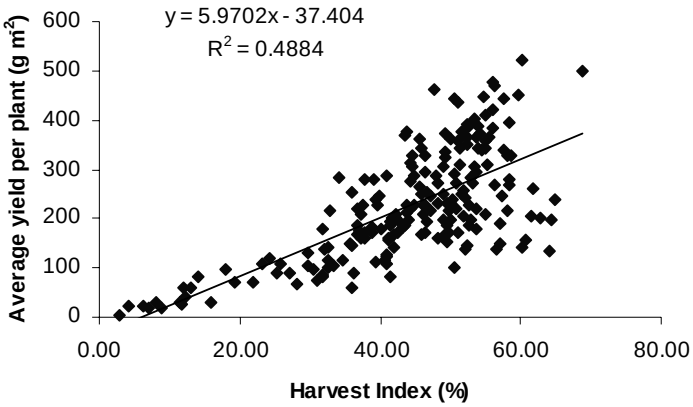

Figure 4-2: Overall correlation between the Harvest Index and yield per plant for landraces grown in controlled experiment under irrigation in 2000 at TCRU, University of Nottingham

After this preliminary analysis of data from the 2000 and 2001 glasshouse seasons, the harvest index emerged as the most important factor influencing differences in yield between landraces. A second point that emerged from the data is that there is an overall good correlation between the total above ground biomass of a plant and its final yield, but variable between the landraces (Figure 4-3 & Figure 4-4) i.e. harvest index is different between landraces and variable within each landrace (Table 4-1).

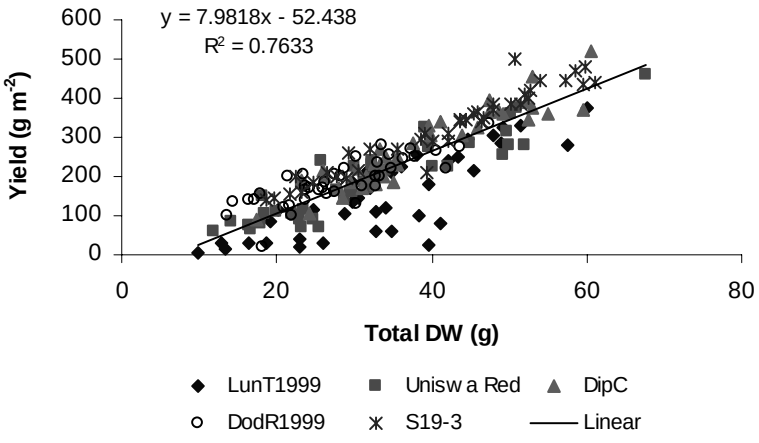

Figure 4-3: Correlation between total above ground biomass and yield per plant for five landraces grown in controlled experiment under irrigation in 2000 at TCRU, University of Nottingham

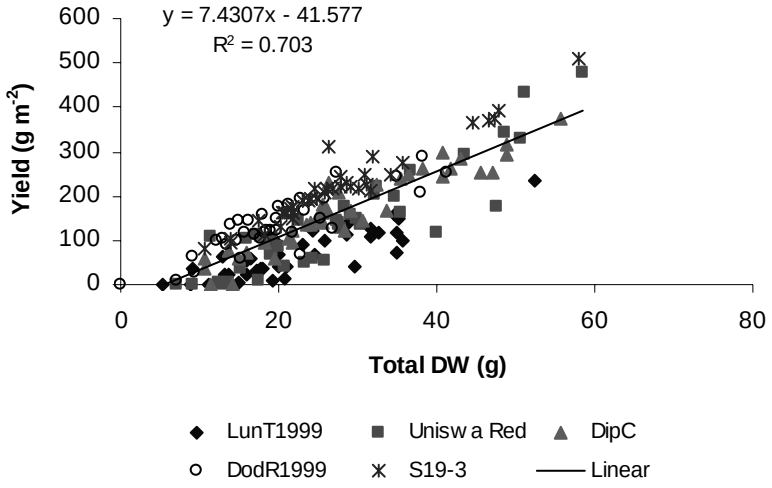

Figure 4-4: Correlation between total above ground biomass and yield per plant for five landraces in controlled experiment under drought in 2000 at TCRU, University of Nottingham

A first step in explaining the differences in harvest index between landraces is considering the yield as a product of average pod weight (W_{pods}, g pod^{-1}) and pod number (N_{pods}, pods m^{-2}):

$$Y = N_{pods} W_{pods}$$

Analysis of available data showed that N_{pods} was highly variable between landraces and across treatments. W_{pods} did vary between the landraces, but was fairly constant, even across treatments (Table 4-2) This agrees with findings in literature. Ofori (1996) states that the number of pods per plants gives the best indication of seed yield status.

Table 4-2: Average number of pods and average weight per pod ± standard error of the mean (average of 10 plants) for five landraces grown in controlled environment experiment at TCRU, University of Nottingham.

		2000		2001	
Landrace	**Treatment**	**Pod number**	**Podweight (g)**	**Pod number**	**Podweight (g)**
Uniswa Red	Irrigated	56 ± 17	0.36 ± 0.07	42 ± 27	0.36 ± 0.10
	Dry	42 ± 19	0.37 ± 0.08	44 ± 18	0.34 ± 0.08
DipC	Irrigated	74 ± 24	0.34 ± 0.07	63 ± 20	0.38 ± 0.07
	Dry	44 ± 9	0.27 ± 0.08	43 ± 14	0.30 ± 0.05
S19-3	Irrigated	62 ± 25	0.41 ± 0.03	72 ± 15	0.47 ± 0.04
	Dry	28 ± 19	0.34 ± 0.03	39 ± 23	0.32 ± 0.06
DodR1999	Irrigated	55 ± 8	0.41 ± 0.14	No Data	No Data
	Dry	17 ± 6	0.60 ± 0.12	No Data	No Data
LunT199	Irrigated	25 ± 15	0.56 ± 0.11	No Data	No Data
	Dry	22 ± 15	0.35 ± 0.18	No Data	No Data

N_{pods} is determined by the number of pegs that grow into pods. However it is very difficult to determine accurately the number of pegs in the field. As bambara groundnut is a self-pollinating crop, and most flowers are fertilised before they open (Massawe *et al*. 2003; Linnemann, 1994), we can assume that most flowers grow into pegs. The pod number (N_{pods}) can then be defined as a function of the number of flowers ($N_{flowers}$) and the proportion (ν) of these flowers that will become pods:

$$N_{pods} = \nu N_{flowers}$$

The constant ν varies between landraces and changes for different growing circumstances (Table 4-3).

Table 4-3: Average number of pods and average number of flowers ± standard error of the mean (average of 40 plants) and proportion of flowers that become pods (ν) for five landraces grown in controlled environment experiment at TCRU, University of Nottingham (2000).

Landrace	Treatment	Pod number	Flower number	ν
Uniswa Red	Irrigated	34 ± 18	65 ± 15	0.53
	Dry	26 ± 20	55 ± 17	0.47
DipC	Irrigated	53 ± 20	73 ± 19	0.72
	Dry	43 ± 19	47 ± 13	0.93
S19-3	Irrigated	51 ± 15	58 ± 14	0.88
	Dry	41 ± 15	51 ± 17	0.81
DodR1999	Irrigated	26 ± 7	60 ± 27	0.44
	Dry	16 ± 10	45 ± 12	0.36
LunT199	Irrigated	19 ± 9	45 ± 19	0.42
	Dry	12 ± 10	73 ± 28	0.17

4.2 WATER LIMITED CROP YIELDS

Low water availability reduces yield in bambara groundnut, as can be seen in Figure 4-5.

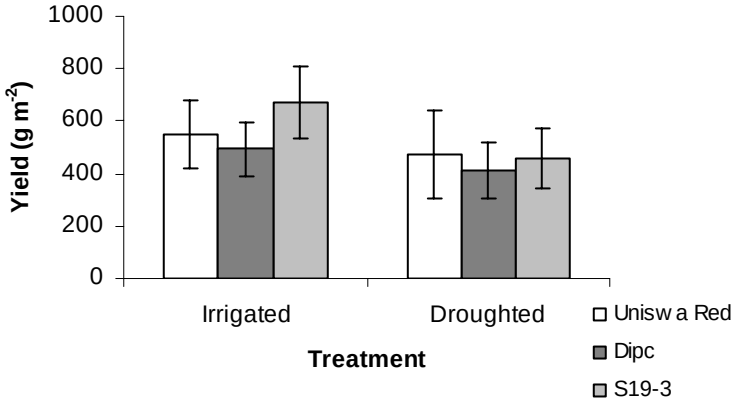

Figure 4-5: Effect of drought on average pod yield per plant for three landraces grown in controlled environment experiment at TCRU, University of Nottingham (2001). Error bars are standard error of the mean (average of 10 plants).

When water is limiting the end of season yield can be expressed as:

$$Y_{wl} = Y * f_{wl}$$

where Y_{wl} is the end of season yield (kg DM ha^{-1} y^{-1}) as affected by water shortage, *Y* is the end-of season yield (kg DM ha^{-1} y^{-1}) as described above and f_{wl} is a land race dependent multiplier reducing the yield. This multiplier is based on the ratio between water supply (i.e. the water availability of the soil) and the potential evaporation.

4.3 PHENOLOGY

Crop duration was divided into five phenological stages. These are Emerging, Vegetative, Flowering, Pod Filling and Maturing (Table 4-4 and Figure 2-4).

Table 4-4: Description of the phases

Stage	Description
Emerging	From sowing until first full leaf above the ground
Vegetative	Start at the end of Emerging until maturity
Flowering	Start at 50% of the crop in flower until maturity (indeterminate)
Pod filling	Start determined by the start of first podding
Maturing	Last phase, end of vegetative phase, crop is senescing

As can be seen in Table 4-4 the Vegetative, Flowering and Pod filling phases overlap each other. As bambara groundnut is an indeterminate crop, leaf production continues even after flowering and podding have started.

Although there might be a wide range in the chronological time taken from a shoot to develop to a specific stage due to environmental factors such as temperature or photoperiod, the amount of phenological time taken is assumed to be constant (Hodges, 1991). Often thermal time is used as a proxy for phenological time. However, in the case of a model for bambara groundnut this is not appropriate, due to the influence on development of photoperiod in addition to temperature. In order to define phenological

time we decided to use the concept of phenochrons. A phenochron is defined as the amount of advancement in the phenological age of the crop over a day when temperature and photoperiod are at their optimum values (Matthews and Stephens, 1998). Thus, the phenological age (A_d, phenochrons) of the crop on day d (days since sowing) is given by:

$$A_d = \sum_{i=1}^{i=n} \left[\frac{(T_d(i) - T_{base})}{(T_{opt} - T_{base})} * f(\phi_d(i)) \right]$$

where n is the number of days experienced by the crop since sowing, $T_d(i)$ and $\phi_d(i)$ are the mean daily temperature (°C) and the photoperiod (h) respectively on day i, T_{base} and T_{opt} are the base and optimum developmental temperatures for a particular growth phase and $f(\phi_d(i))$ is a function relating daily photoperiod to a zero-to-unity multiplier (Matthews and Stephens, 1998). The function used in this study can be seen in Figure 4-6. The number of phenochrons required to reach a specific stage of development is a constant.

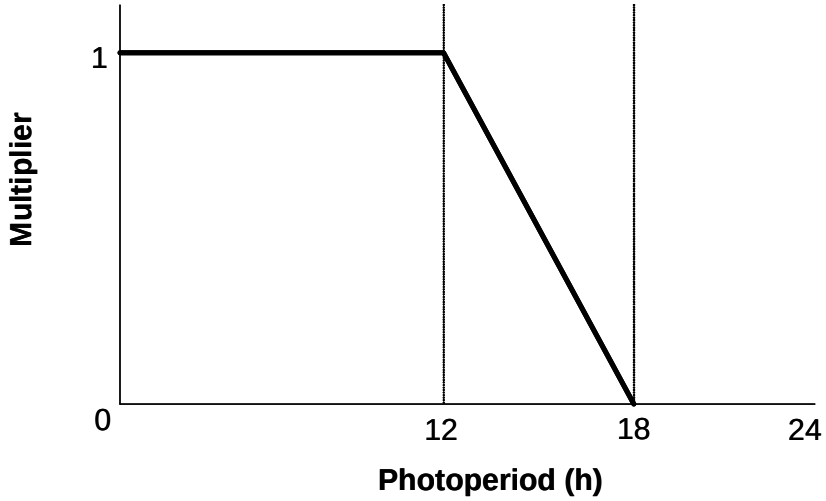

Figure 4-6: Function relating daily photoperiod to a zero-to-unity multiplier.

4.4 DIFFERENCES IN LEAF APPEARANCE BETWEEN GLASSHOUSE AND FIELD

One of the major problems in developing the model (BamGro), was the different observed rate of leaf appearance and consequent rate of leaf area development between the glasshouse and the field (Figure 4-7 and Figure 4-8).

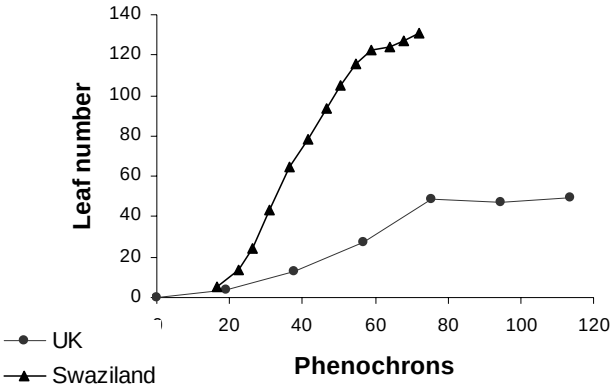

Figure 4-7: Relation between number of leaves per plant and time (phenochron) for Uniswa Red in the TCRU glasshouses, UK and the Malkerns field site, Swaziland.

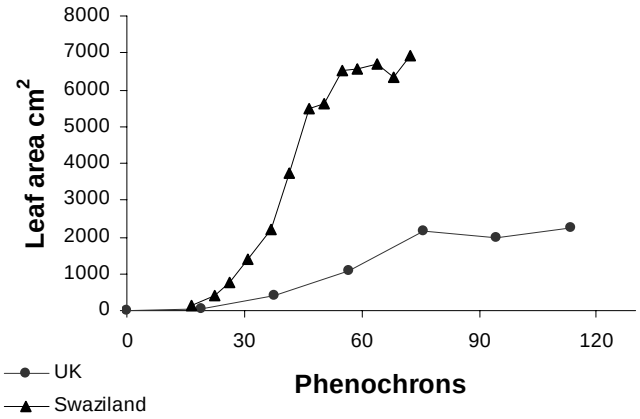

Figure 4-8: Relation between leaf area development (cm^2) per plant in time (phenochron) for Uniswa Red in the TCRU glasshouses, UK and at the Malkerns field site, Swaziland.

When the relation between leaf area per plant and leaf number per plant is observed (Figure 4-9), there is no difference between the UK and Swaziland. The differences between the field and the glasshouse are therefore more likely to be the result of an effect of environment on the leaf initiation.

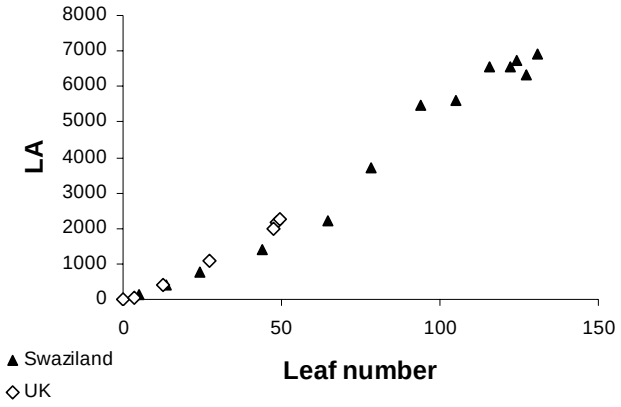

Figure 4-9: Relation between leaf area development (cm^2) per plant and leaf number per plant for Uniswa Red in the TCRU glasshouses, UK and at the Malkerns field site, Swaziland.

In situations where water, nutrients and photoperiod are non limiting, leaf appearance is considered to be dependent on temperature only (Azam-Ali and Squire, 2002). Many studies show that for a given genotype and environment, the rate of leaf appearance is linear with thermal time (Massawe *et* al., 2003; Qi *et al*., 1999; Volk and Bugbee, 1991; Masle *et al.*, 1989; Cao and Moss, 1989).

In this study the leaf appearance rate was typically three times higher in the field, than in the glasshouse for the same landrace. Robertson *et al.* (1998) warn that relationships between temperature and canopy development are difficult to determine from field data alone, because of the daily fluctuations in air temperature. The average air temperature in the glasshouse was a constant 27 ^{o}C, with a diurnal amplitude of 5 °C throughout the season. In contrast the average air temperature in the field fluctuated on a daily basis and ranged from 17 to 27 ^{o}C.

Massawe *et al*. (2003) reported an increase of leaf appearance rate with elevated mean temperature from 20 to 32.5 °C, but a decrease at a constant mean temperature of 35 °C. This suggest that the optimum temperature for leaf appearance rate is between 32.5 and 35 °C. As a result the lower average air temperature in the field does not explain the higher leaf appearance rate compared to the glasshouse, it points to other differences in environmental conditions that may influence the leaf appearance.
Photoperiod is reported to influence the leaf appearance of different species (Azam-Ali and Squire, 2002; Slafer and Rawson, 1997; Baker *et al*., 1980). The photoperiod was controlled at 12 h in the glasshouse, throughout the reproductive phase, whilst during the growing season in Swaziland the photoperiod ranged between 11h and 14 h. Furthermore, studies (Brink, 1999; Brink, 1997) have shown that the rate of change in daylength both from short to long and long to short days influence pod initiation. It is not clear if a similar mechanism occurs in leaf initiation, either independently or as a result of pod initiation.

Planting density and the increase in competition for resources has an effect on leaf number (Edje *et al*., 2003; Sesay and Yarmah, 1996; Karikari *et al.*, 1996). The planting density in the glasshouse is 15 plants m^{-2}, while in the field the spacing is 6.7 plants m^{-2}. This difference of more than double the planting density can have an influence on the leaf number when the canopy is closing, however it is unlikely to influence the leaf appearance rate early in the season, when the plants are not yet competing over the available resources.

Finally there is a difference both in quantity and quality of light received by the plants in the glasshouse and the plants in the field. The mean irradiance in the UK is lower than in Swaziland (radiation receipt over the 2003 growing season of 1220 MJ in the glasshouse and 2360 MJ in the field) , further more the glass and structure of the glasshouse absorb a large proportion of the incoming radiation. Recent studies show an effect of both light quality (Rajean *et al*., 2002; Gautier and Varlet-Grancher, 1996) and quantity (Rajean *et* al., 2002; Bertero, 2001) on the rate of leaf appearance in crops.

More research is needed on how the leaf appearance rate is influenced by temperature, photoperiod, planting density and both light quantity and quality.

4.5 END-USERS AND INTERFACE

One of the aims during the development of the model, was to make it as accessible to future end-users as possible (see also Chapter 10). Surveys of Decision Support Systems reported by Greer *et al.* (1995) suggest that the complexity of the user interface is one of the most limiting factors in their uptake. Other authors (Newman *et al.*, 2000; Knight, 1997) agree that a clear and easy to use interface is important.

BamGro has been written in Delphi and a user-friendly interface could be linked to the model. This should be a MS Windows based program, which will be easy to understand with basic computer skills and should be fully compatible with the latest MS Windows versions.

An example of such an interface was developed and presented on the International Bambara Groundnut Symposium, Botswana College of agriculture, Botswana, 8-12 August 2003 (Figure 4-10). This interface has not been linked to the model.

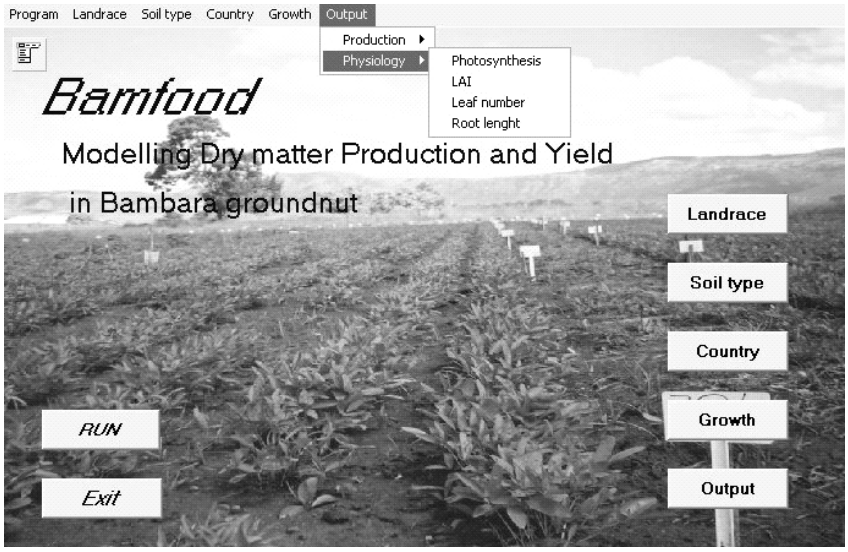

Figure 4-10: An example of an interface end for the model (Cornelissen *et al*., 2003).

CHAPTER 5 EFFECT OF SPACING ON BAMBARA GROUNDNUT

5.1 INTRODUCTION

Sowing density has an important effect on the yield of bambara groundnut (Sticksel *et al*., 2002). For modelling purposes, it is important to quantify this influence.
In Chapter 4 the yield is considered as a product of average pod weight and average pod number. In this Chapter the effect of spacing on both pod number and podsize is studied.

Field observations show that pods develop better when formed underground. It is therefore likely that the growth habit of a landrace has an effect on the development of pods, under optimum growing conditions, spreading landraces are likely to have more and better developed pods than erect ones (Edje *et al*., 2003; Elia, 1985). Spacing has an influence on the growth habit of the plant, as lower planting densities lead to more space for individual plants. It can be expected that plants will grow larger and have a more spreading habit under lower planting densities than when planted under high densities (Edje *et al*., 2003; Sesay and Yarmah, 1996; Karikari *et al.*, 1996).

To validate these assumptions, the following hypotheses have been tested in the field:

1. The growth habit of the plant has an effect on the development of pods (a spreading plant with soil contact will produce more pods than an erect plant where pegs are not in close contact with the soil) and the growth habit is influenced by plantspacing.
2. Spacing has a significant effect on pod number (this is a combined effect of higher competition between plants and a change in the growth habit of the plant). The number of pods does have a significant effect on yield differences between plants.
3. Spacing has a significant effect on pod diameter. The diameter of pods does not have a significant effect on yield differences between plants.

5.2 MATERIALS AND METHODS

Three landraces were sown on 11 January 2002 at Malkerns Research Station, Swaziland under three different spacings. The landraces were: OM1, a landrace expected to spread, SB16-5A, an intermediately spreading landrace and AHM698, a landrace with a compact growth habit.

Three replicates of nine plots were square planted with the following spacing: 22*22 (20.7 plants m^{-2}), 45*45 (4.9 plants m^{-2}) and 60*60 (2.8 plants m^{-2}). The design of the experiment was a fully randomised block with three replications, with the size of the plots being determined by the number of plants in the plot (see Plate 5-1). The plots needed to have at least ten plants in the centre of the plot for measurements, and a guard row of at least 1 plant on all the edges. All plots were fertilized with NPK compound fertilizer (2-3-2) at a rate of 500 kg ha^{-1} before planting, and were hand-weeded regularly to keep weed pressure low. Cutworm bait (KOMBAT – Sodium Fluosilicate) was applied along the rows upon emergence and the plants were sprayed with an insecticide (Malathion) and fungicide (Eria 187,5 SC Novartis South Africa; difenoconazole (triazole) and carbendazim) using a knapsack sprayer, as necessary to control aphids and diseases

Plate 5-1: Experimental layout of the bambara groundnut experiment at Malkerns Research Station, Swaziland

Every two weeks, the length (measured along the row), width (measured across the row) and height of ten selected plants in each plot were measured. Three plants were selected in every plot, and the total number of leaves on each was counted weekly. On the same plants, the total number of flowers was recorded twice a week. Because of the duration of the stay by the author, these measurements could only be made until April 15 (94 DAS). At this time, the plants were filling pods, but had not yet reached maturity. Usually maturity is assessed in the field, but takes at least 4 months for the selected landraces (i.e. ~May 11, 120 DAS).

Two detailed growth analyses were made, the first on April 12 (91 DAS), and the other at the end of the season (May 23, 132 DAS) to determine the final productivity. For each of these growth analyses, the following measurements were taken: total number of leaves, total number of pods, length and width of five middle leaflets, diameter of five selected pods (only on April 12) and total above ground dry weight. All data were analysed on a per plant basis. The leaf area of each plant was estimated using its total leaf number and the length and width of five middle leaflets (Cornelissen *et al*., 2002).

Statistical analysis was done using Genstat, (VSN International Ltd) using a standard analysis of variance (ANOVA).

5.3 RESULTS

5.3.1 Leaves

Statistical analysis (ANOVA, $p<0.05$) of the results showed a significant influence of plant spacing on leaf number per plant, when the 22*22 cm spacing was compared with the 45*45 cm spacing. The the 45*45 cm spacing always had a higher number of leaves per plant, than the 22*22 cm spacing. However, there was no significant effect of plant

spacing on average leaf number per plant ($p<0.05$) when the 45*45 cm spacing was compared to the 60*60 cm spacing (Figure 5-1).

There was a significant effect of landrace on the average leaf number per plant. There was also a significant interaction between landrace and spacing on leaf number per plant (Figure 5-1).

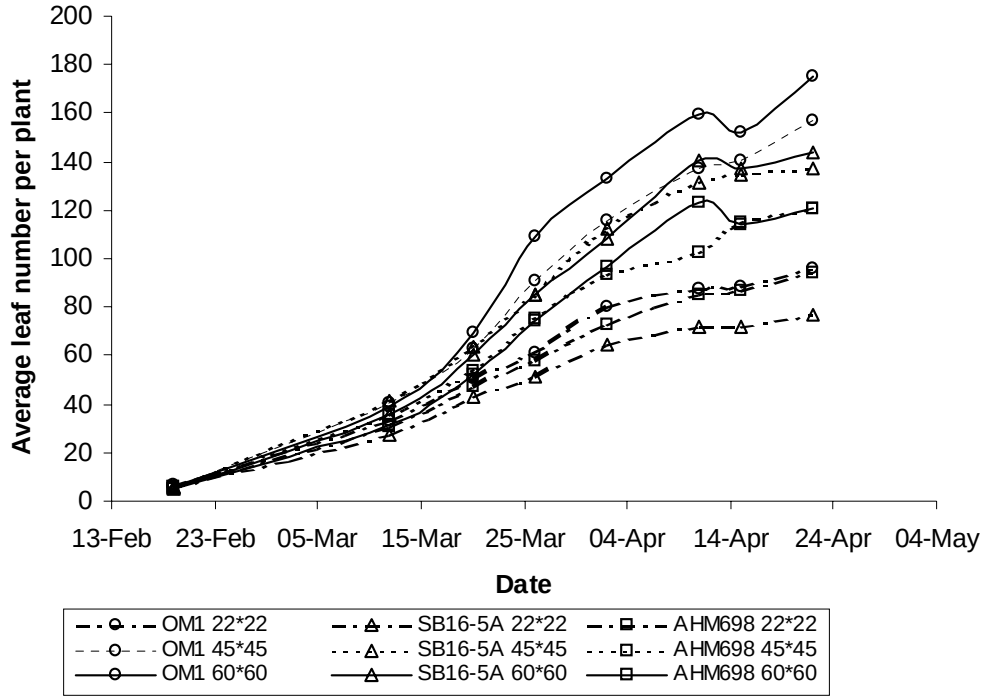

Figure 5-1: Effect of spacing on the average number of leaves per plant in time for three landraces

The variation in number of leaves between plants does not change during the growth period. OM1 and AHM698 have the highest variation (Table 5-1). The variation between plants within the same landrace is reduced as the spacing increases.

Table 5-1: Average coefficient of variation for number of leaves per plant from 19 Feb to 22 Apr. (± standard deviation), n = 10.

Landrace	Spacing	*Coefficient of variation*
OM1	22*22	0.30 ± 0.05
OM1	45*45	0.20 ± 0.03
OM1	60*60	0.19 ± 0.06
SB16-5A	22*22	0.19 ± 0.02
SB16-5A	45*45	0.11 ± 0.03
SB16-5A	60*60	0.19 ± 0.07
AHM698	22*22	0.27 ± 0.05
AHM698	45*45	0.20 ± 0.04
AHM698	60*60	0.13 ± 0.02

5.3.2 Flowers

When the 22*22 cm spacing was compared to the 60*60 cm spacing, statistical analysis (ANOVA, $p<0.05$) showed a significant effect of spacing on the cumulative number of flowers for OM1 and SB19-5A. The the 60*60 cm spacing always had a higher cumulative number of flowers per plant, than the 22*22 cm spacing. However, spacing did not seem to affect the cumulative number of flowers for AHM968 (Figure 5-2).

There was a significant effect of landrace on cumulative numbers of flowers per plant (ANOVA, $p<0.05$) when the 45*45 cm spacing is compared with the 60*60 cm spacing (Figure 5-2). However spacing only seemed to have a significant effect on OM1 when grown at low densities.

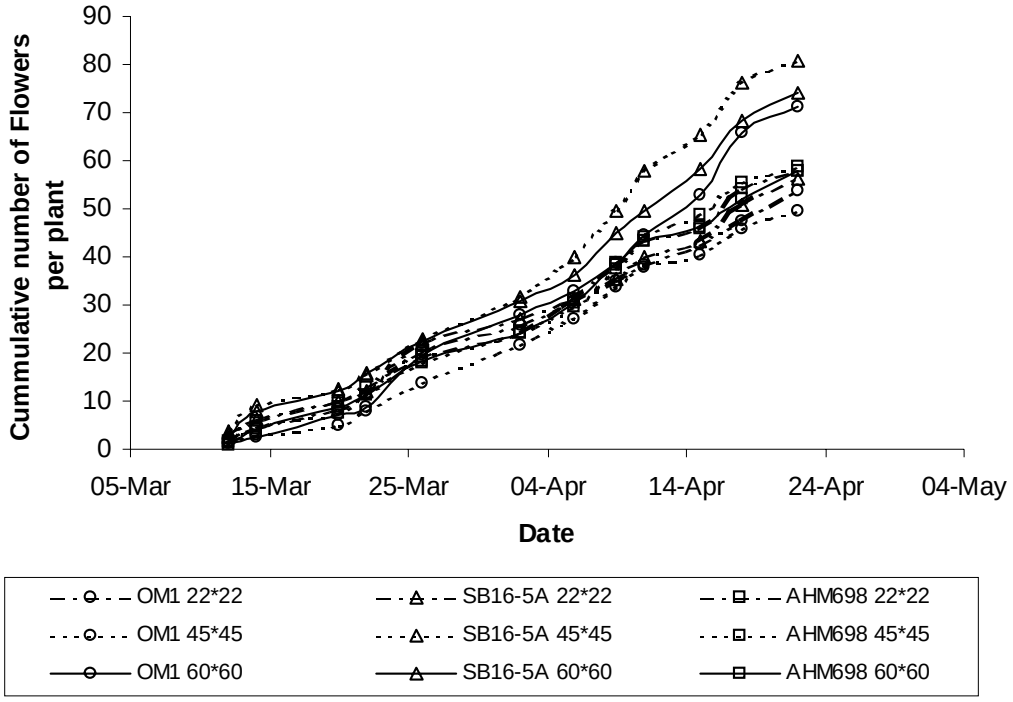

Figure 5-2: Effect of two planting densities on cumulative number of flowers per plant for three landraces.

The variation in the number of flowers between plants is high in the first stages, after the first 10 days, the variation decreases and stabilises to between 0.14 and 0.41. This explains the high CVs observed (Table 5-2). As for the leaves number, there is more variation between plants for landraces OM1 and AHM698 than for SB16-5A.

Table 5-2: Average coefficient of variation for cumulative number of flowers per plant from 12 Mar to 22 Apr. (± standard deviation), n = 10.

Landrace	*Spacing*	*Average coefficient of variation*		
OM1	22*22	0.46	±	0.30
OM1	45*45	0.51	±	0.22
OM1	60*60	0.43	±	0.23
SB16-5A	22*22	0.23	±	0.06
SB16-5A	45*45	0.22	±	0.15
SB16-5A	60*60	0.34	±	0.13
AHM698	22*22	0.40	±	0.18
AHM698	45*45	0.41	±	0.31
AHM698	60*60	0.39	±	0.32

5.3.3 Growth-Analysis

Results showed that there was a significant effect (ANOVA, $p<0.05$) of plant spacing on leaf area per plant (Figure 5-3), total leaf number per plant (Figure 5-4), and total above ground dry weight per plant (Figure 5-5) at both growth analyses.

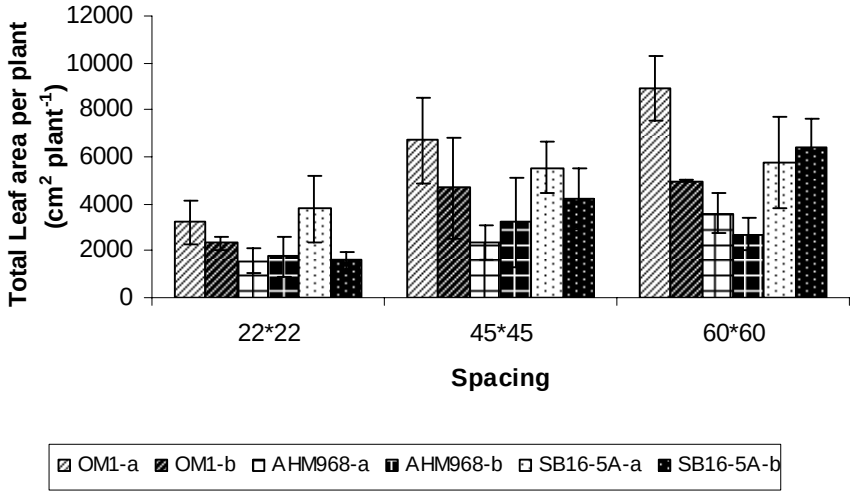

Figure 5-3: Effect of spacing and landrace on total leaf area per plant for two sampling dates (a = 12 April 2002, b = 23 May 2002), the results are an average of 10 plants, error bars are standard error of the mean.

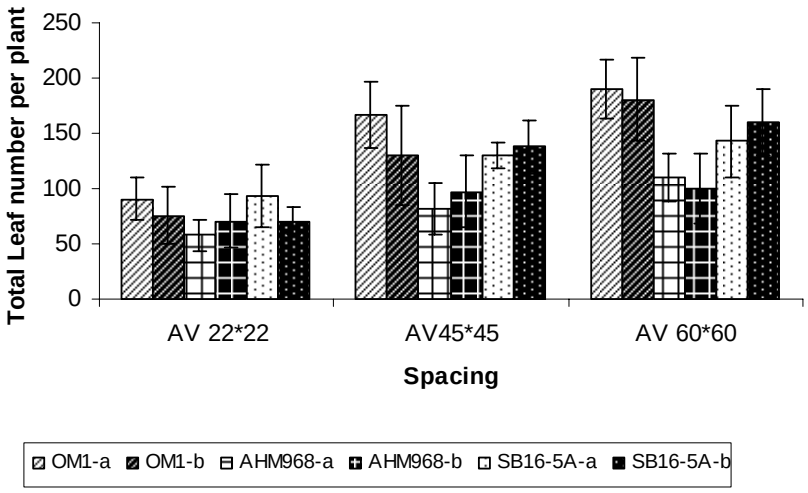

Figure 5-4: Effect of spacing and landrace on total leaf number per plant for two sampling dates (a = 12 April 2002, b = 23 May 2002), the results are an average of 10 plants, error bars are standard error of the mean.

More leaves were formed at the lower densities than in the 22*22 spacing - in all cases, there was no difference in the number of leaves between the 45*45 and 60*60 spacings. The total number of leaves per plant and the total leaf area per plant were higher for some landraces in the first growth analysis than in the second, which was probably because maturity had been reached and the plants had started senescing by the time of the final harvest. Significant differences in total leaf number, leaf area, and total dry weight were found between landraces.

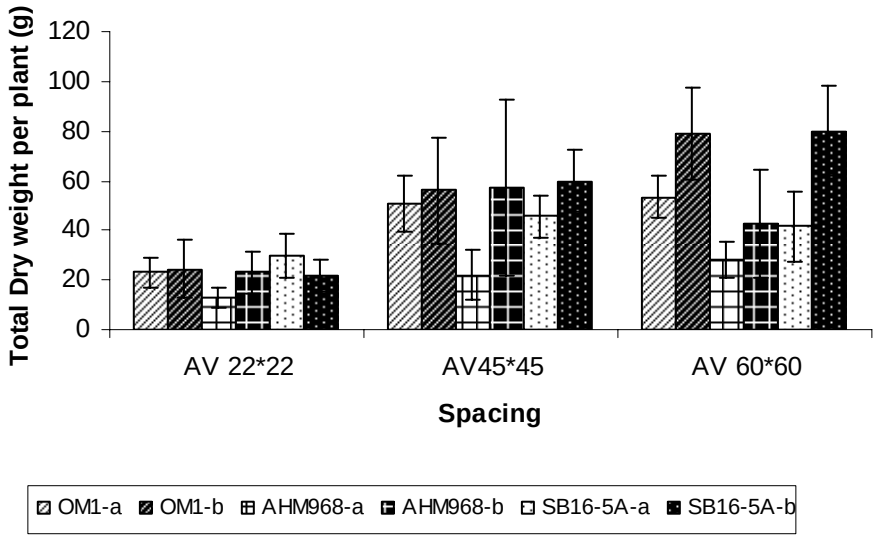

Figure 5-5: Effect of spacing and landrace on total above ground dry weight per plant for the two sampling dates (a = 12 April 2002, b = 23 May 2002), the results are an average of 10 plants, error bars are standard error of the mean.

In both growth-analyses, a significant effect (ANOVA, $p<0.05$) of spacing on total pod number was found. Although AHM968 seemed to produce the least pods at every density, statistical analysis did not show a significant effect of landrace on the total pod number (Figure 5-6).

Statistical analysis (ANOVA, $p<0.05$) of pod size in the first growth analysis shows a significant effect of both spacing and landrace on the pod diameter. Larger pods were found in the lower plant densities. Sb16-5A had the largest pods (Figure 5-7).

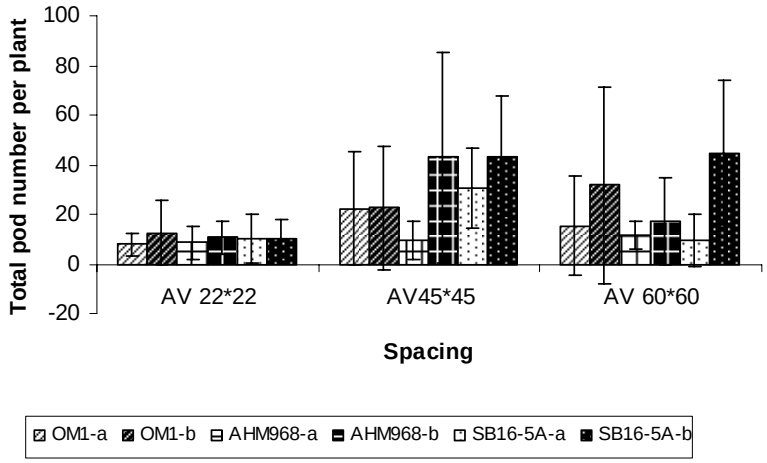

Figure 5-6: Effect of spacing on total pod number per plant for the two sampling dates (a = 12 April 2002, b = 23 May 2002), the results are an average of 10 plants, error bars are standard error of the mean.

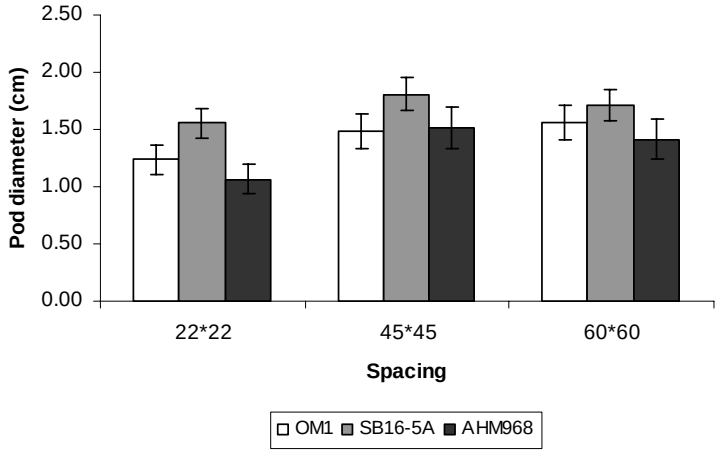

Figure 5-7: Effect of spacing and landrace on pod size per plant for the 12 April 2002 sampling date, the results are an average of 10 plants, error bars are standard error of the mean.

5.3.4 Length and width

The plant length and width measurements were consistent with the findings of the growth analyses. The largest plants were found in the 45*45 and 60*60 spacings. Because of the square planting, the length and width measurements show similar trends (Figure 5-8 and Figure 5-9).

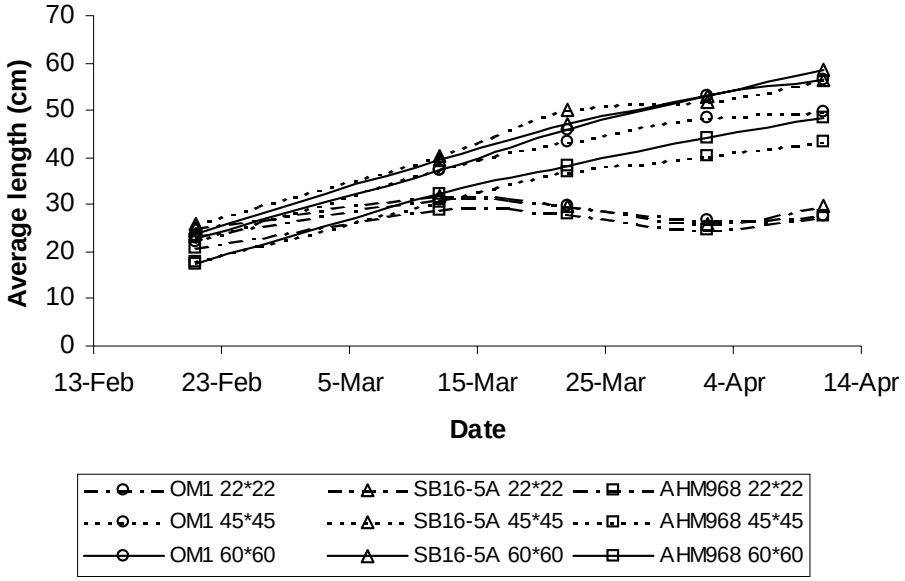

Figure 5-8: Effect of spacing and landrace on plant length (2002).

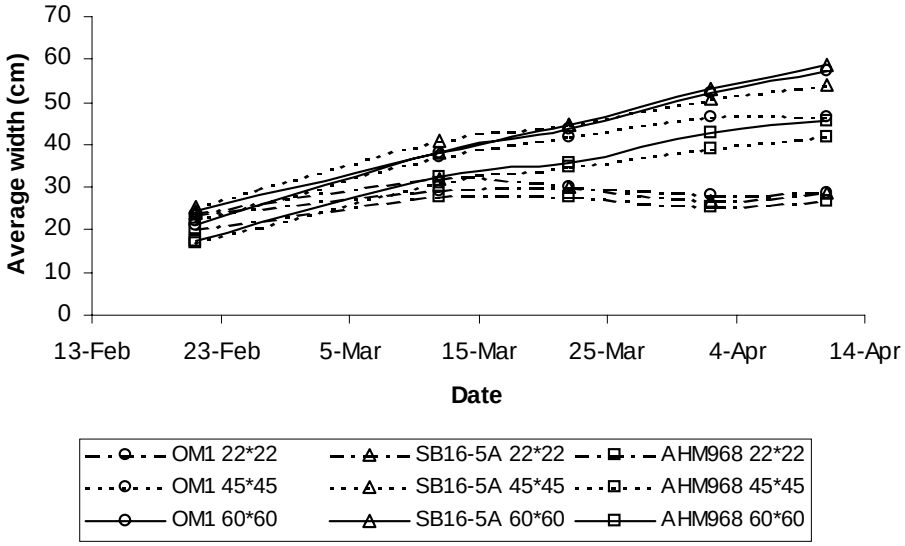

Figure 5-9: Effect of spacing and landrace on plant width (2002).

AHM968 was statistically (ANOVA, $p<0.05$) the smallest (least spreading plant) in the experiment. There was no significant difference in size between OM1 and SB16-5A.

Variation between leaves (within and between plants) length and width is low and relatively stable in time (Table 5-3). All landraces appear to have a similar level of variation and spacing appear to have little influence.

Table 5-3: Average coefficient of variation for average leaves length and width from 21 Feb to 11 Apr. (± standard deviation), n = 10.

		Length			*Width*		
Landrace	*Spacing*	*Average of variation*		*Coefficient*	*Average of variation*		*coefficient*
OM1	22*22	0.10	±	0.05	0.05	±	0.05
OM1	45*45	0.12	±	0.02	0.14	±	0.03
OM1	60*60	0.03	±	0.01	0.04	±	0.01
SB16-5A	22*22	0.05	±	0.03	0.07	±	0.05
SB16-5A	45*45	0.09	±	0.04	0.06	±	0.01
SB16-5A	60*60	0.05	±	0.02	0.05	±	0.02
AHM968	22*22	0.11	±	0.05	0.08	±	0.05
AHM968	45*45	0.06	±	0.02	0.04	±	0.03
AHM968	60*60	0.08	±	0.03	0.09	±	0.04

5.4 DISCUSSION

AHM968 showed the least response to a lower planting density, which can be explained by its compact bunchy type growth habit and inability to spread. Providing more space per plant, therefore, would not be expected to affect the growth habit of this landrace. OM1 showed the strongest response to a lower planting density, which can be explained by its spreading growth type.

Sticksel *et al.* (2002) report an inverse relation between plant spacing and yield components (number of pods per plant, average plant yield). This study shows that there is a clear reduction of average plant yield at the 22*22 cm spacing. The effect is less clear and not always statistically significant when the 45*45 cm spacing is compared

with the 60*60 cm spacing. Two reasonable explanations can be given for this response to sowing density. The 22*22 cm spacing is extremely dense and besides competing for physical space the plants also compete for light and nutrients. Secondly, it might be that the landraces used in this experiment reach their maximum spread in the 45*45 cm spacing and cannot use the extra space provided in less dense populations. This seems to be supported by the evidence that when the 60*60 cm spacing is compared to the 45*45 cm spacing no significant effect of the increase in plant length can be found (Figure 5-6).

Studies show that bambara groundnut is normally grown by farmers using planting densities of 0.3 to 16 plants m^{-2} (Brink *et al.*, 1996; Sesay *et al.*, 1996; Mabika and Mafonga, 1997; Nambou, 1997). The 45*45 cm (4.9 plants m^{-2}) and the 60*60 cm (2.8 plants m^{-2}) spacings fall within this range, while the 22*22 cm (20.7 plants m^{-2}) spacing is much more dense.

When studying spacing experiments two things have to be considered: the increase of productivity per plant under lower plant densities and the increase of total yield on a per area basis under a higher planting density. These often interact leading to a range of optimum planting densities where an increase or decrease of plants per m^2 has limited effect. In this experiment, a positive effect of spacing on the size of the pods was found (the diameter increases under lower planting densities). An explanation could be that in the lower planting densities the developing pods could easily reach the soil surface, due to the more spreading growth habit of the plant, leading to a better development. On the other hand it could be just that individual plant growth is better in the lower planting densities, due to less competition for light, space and nutrients, resulting in better pod growth.

Contrary to usual practice, the plants in the experiment were not earthed up. Earthing up is considered to have a beneficial effect on pod development (Balole *et al*., 2003; Sesay *et al.*, 1999, Swanevelder, 1998).

5.5 CONCLUSIONS

1. Spacing has a significant effect on pod diameter, but there is no significant correlation between the size of pods and total pod weight per plant.
2. Pod number seems to be the most important factor determining yield. However a difference in pod numbers per plant between the landraces studied could not be found.
3. Although plants do have a more spreading growth habit under lower planting densities, it is difficult to determine if the influence of spacing is a result of a change in the shape of the plant or a decrease in competition for resources as light and nutrients.
4. Spacing has a significant effect on pod number, total leaf number and total flower number.

CHAPTER 6 GAS-EXCHANGE IN BAMBARA GROUNDNUT

6.1 INTRODUCTION

In Chapter 4 it was assumed that pod number is the most important factor influencing the yield of bambara groundnut. In this Chapter the assumption that there are no differences in gas-exchange between landraces is studied.

Gas exchange is one of the most important factors determining potential plant production. Plants use carbon dioxide, through photosynthesis, to produce biomass. The potential rate of photosynthesis and the response of plants to changes in light intensity is an important characteristic of a plant species.
Moreover, the photosynthetic behaviour of a plant is a basis for many simulation models describing plant growth or differences between different varieties of a species. Plant architecture has an influence on rates of gas exchange, due to the position of leaves in the canopy and the resulting amount of light that can reach the leaves (e.g. Azam-Ali and Squire, 2002; Lawlor, 2001; Gratani and Bombelli, 1999). Gas exchange measurements on single leaves have the ability to investigate the actual photosynthetic efficiency of the plants without any bias due to the shape of the plant, and have often been used to compare either *species* (e.g. Horton *et al*, 2001; Stafne *et al*, 2000; Gratani and Bombelli, 1999; Singleton-Jones, 1998; Da Matta *et al*, 1997; Apel and Peisker, 1995;) or *cultivars* of a species (e.g. Leidi *et al*, 1999, Srinivas *et al*, 1999; Sexton *et al*, 1997; Pettigrew and Meredith, 1994; Pettigrew *et al*, 1993).

The photosynthetic activity of a plant or an organ is dependent on the amount of energy received; the energy used for photosynthesis is the visible light (i.e. with wavelengths between 400 and 700 nm) and is often called Photosynthetically Active Radiation (PAR). The response of photosynthesis to an increase of light intensity is not linear: limiting factors appear (mainly due to a limitation in the rate of dark reactions), with the result that the assimilation of CO_2 reaches a plateau at high light intensity (see Figure

6-1). A light response curve can be obtained by making gas exchange measurements (and in particular the net photosynthesis) at different light intensities, while keeping all other influencing factors (CO_2 concentration, hygrometry, temperature, water status and plant age) constant.

Gas-exchange information on bambara groundnut should lead to a better understanding of the photosynthetic activity of the species, in particular the contribution of single leaves to resource use and conversion, or the effect of drought on carbon assimilation and water economy. Such information could also be useful for breeding and the development of cultivars for new areas, although photosynthetic characteristics seem very difficult to manipulate in breeding programmes (Joshi, 1997). However, Udayakumar (1994) has reported that different unimproved germplasm of a single species can show higher photosynthetic rates.

Differences in photosynthetic behaviour between landraces might be expected as a result of their different origins and their large variation in anatomical appearance, and the fact that the species is grown across a wide range of latitudes and environments. However, landraces have not originated from selected individuals but from selected populations, so intra-landrace variability can also be great.

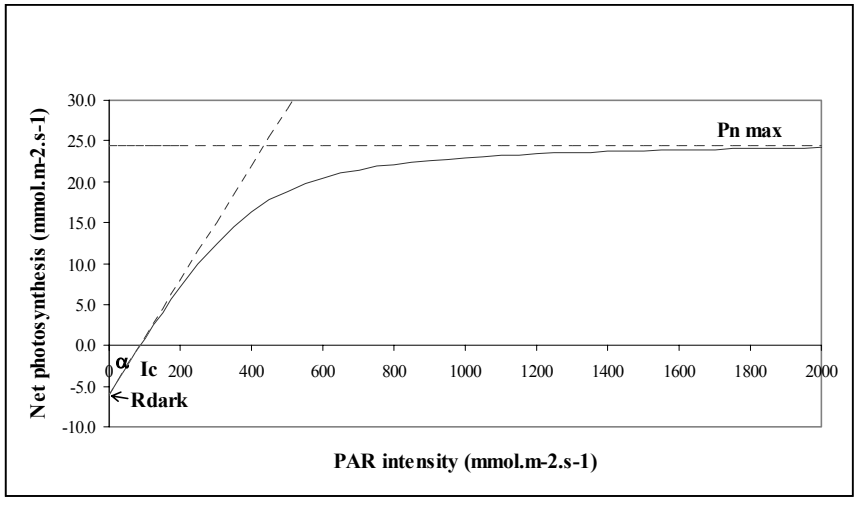

Figure 6-1: Schematic photosynthesis-light response curve showing the dark respiration (R_d), light compensation point (lc), quantum yield (α) and maximum rate of net photosynthesis ($P_{n,max}$) (adapted from Iqbal *et al.* 1997)

6.2 MATERIALS AND METHODS

6.2.1 Experimental set-up

Two sets of experiments were conducted in order to determine the light response curve in three bambara groundnut landraces.

Experiment 1 is the pot experiment (as described in Chapter 3). The plants were grown without drought stress. However the light intensity received by the plants between measurements was low because of the time of year (March/April). Experiment 2 is the glasshouse main experiment described in Chapter 3. Plants were grown in irrigated plots and plots under a drought regime. The effect of water stress could be determined.

6.2.2 Measurements and data analysis

6.2.2.1 Gas-exchange

In the Experiment 1, eight plants of every landrace were selected for non-destructive measurements of leaf number. From these plants, two leaves (10^{th} and 60^{th} leaves) were selected and tagged. The first set of leaves were tagged at the beginning of the experiment and used for measurements until 60 DAS (early leaves). The second set of leaves were tagged after 60 DAS and used for measurements until the end of the experiment (late leaves). In the second experiment, three plants were selected in every plot to give a total of six plants per landrace. From these plants, one leaf was tagged and followed till the end of the experiment.

To determine the light response curve of a leaf, a portable Infra Red Gas Analysis (CIRAS-1, PP-systems, UK) system was attached to the middle leaflet of a chosen leaf, using a cuvette with a measuring area of 2.5 cm^2. Different light intensities were obtained by attaching an artificial light source to the top of the cuvette. Both the cuvette

and the light source have a fan, reducing the risk of the leaf heating up. The use of different combinations of filters and a diffuser allowed light intensities of between 20 and 2000 μmol PAR m^{-2} s^{-1}. The CO_2 concentration in the cuvette was set at 350 ppm. The measurements were taken every two weeks on the same leaflet to determine the changes in gas exchange over time. There was no visible indication of long term damage to the leaf.

6.2.2.2 Chlorophyll content

At the same time as the gas exchange measurements were being made, a portable chlorophyll meter (Minolta SPAD-502) was used to measure the 'greenness' of the leaflet. Two point measurements were taken on both sides of the midrib in the sampling area of the CIRAS cuvette and averaged.

In order to relate the SPAD value to the actual chlorophyll content of the leaf, 20 middle leaflets of each landrace (S19-3, Diphiri Cream and Uniswa Red) were selected. The leaflets were chosen to represent a large range of colour (for this purpose, some plants were put in the dark for 5 d, in order to induce some leaf chlorosis). Then, SPAD measurements were made on the selected leaves (average of four measurements per leaflet). The extraction of the chlorophyll was performed following a slightly adapted version of the method described in Marquard and Tipton (1987): five 3 mm^2-disks were taken in each leaflet, weight and immersed in 10 ml *N,N*-dimethylformamide (DMF), and put immediately in the dark. The absorbance was measured 24 h later, using a spectrophotometer, at 647 and 664.5 nm.

The chlorophyll content was determined using the empirical equations published in Inskeep and Bloom (1985):

$$\text{Total Chlorophyll (mg l}^{-1}) = 17.9*Abs_{647nm} + 8.08*Abs_{664.5nm}$$

$$\text{Chlorophyll a (mg l}^{-1}) = 12.7*Abs_{664.5nm} - 2.79*Abs_{647nm}$$

$$\text{Chlorophyll b (mg l}^{-1}) = 20.7*Abs_{647nm} - 4.62*Abs_{664.5nm}$$

The data analysis was performed with Genstat (analysis of variance on the Chlorophyll a/ Chlorophyll b ratio (referred to as Chl a/Chl b hereafter)), and with Excel (regression and comparison of regressions for the calibration of the SPAD meter).

6.2.2.3 Light-response curve model

After taking the measurements, a model describing the relationship between photosynthetic activity of a single leaf and incident light intensity was adjusted to the mean values of the data set, according to the landrace, the leaf number, and the period of the measurement (early and late in the first experiment). An exponential model was used, as presented by Iqbal *et al.,* (1997) [see Figure 3.12], and used by Jensen *et al.,* (1998):

$$P_n = P_{g,\max}\left[1 - e^{-(\alpha . I / P_{g,\max})}\right] - R_d$$

where:

P_n: the net photosynthesis rate (μmol CO_2 m^{-2} s^{-1})

α: the slope of the curve at low light intensity (i.e. the quantum yield) (μmol CO_2 μmol PAR)$^{-1}$

I: the PAR intensity incident on the leaf (μmol CO_2 m^{-2} s^{-1})

$P_{g,\max}$: the maximum rate of photosynthesis (μmol CO_2 m^{-2} s^{-1})

R_d: dark respiration (μmol CO_2 m^{-2} s^{-1})

Moreover, saturating irradiance I_s (defined as the intensity giving P_n=95% $P_{n,max}$) was also calculated.

Light response curves for individual plants were compared using the method of comparison of regression lines described in Mead *et al.,* (1993) and Tranchefort (1974).

6.3 RESULTS

6.3.1 Chlorophyll content

The relationship between SPAD values and measured chlorophyll concentrations; both linear and second-degree polynomial, were tested and are shown in Figure 6-2. The linear model gave a good correlation between observed and predicted values (R^2=0.95, see Figure 6-2), with the advantage of complete linearity between the SPAD value and chlorophyll content, which is important in case of averaged data. Nevertheless, this model was biased. A comparison of regression between the linear and the polynomial model showed that the latter was a significantly better fit (F=14.75*).

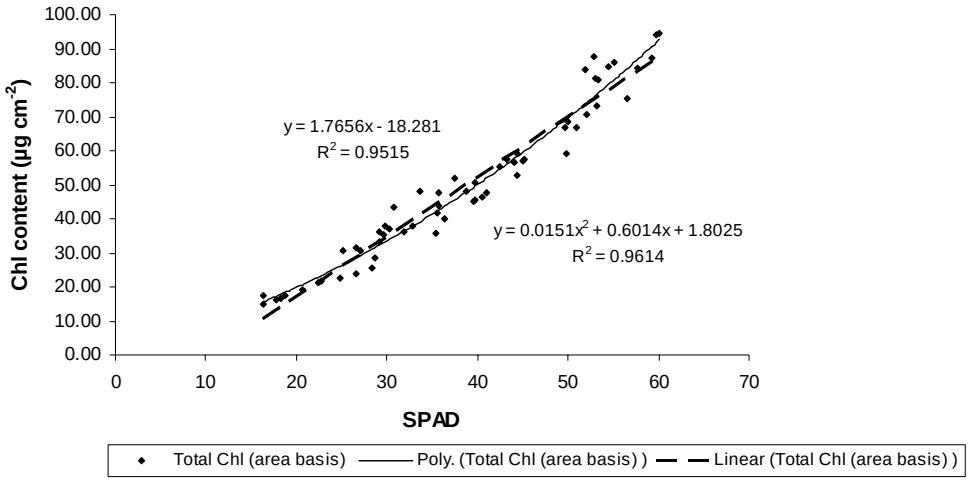

Figure 6-2: Relation between total Chlorophyll content (area basis) and SPAD value for all three landraces

A comparison of regression lines demonstrated that there was no significant difference between the three landraces S19-3, Diphiri Cream, and Uniswa Red in terms of the relation between SPAD reading and total chlorophyll concentration.

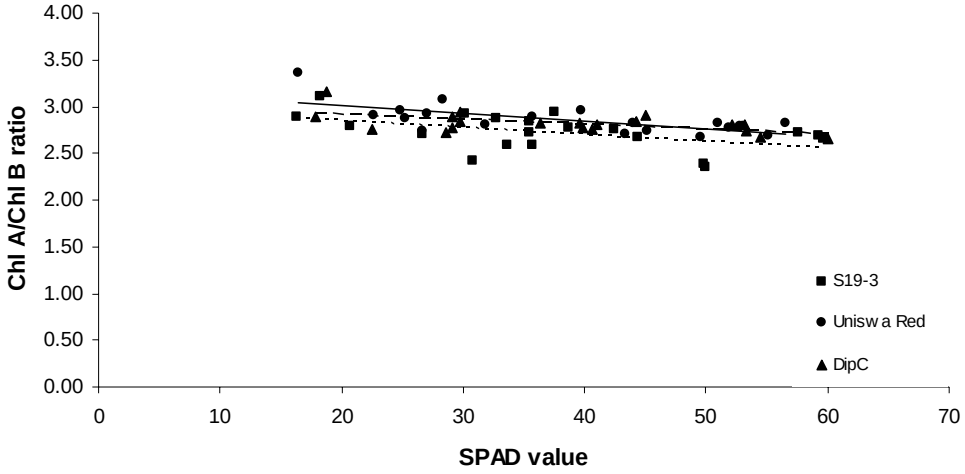

Figure 6-3: Relation between Chlorophyll A/Chlorophyll B Ratio and Total Chlorophyll (represented as SPAD value) concentration. The slope of the line is significant (F=19.3***) Uniswa Red: y = -0.0083x + 3.1; S19-3: y = -0.0073x + 2.9; DipC: y = -0.0051x + 3.0.

Figure 6-3 demonstrates that the nature of total chlorophyll did not appear to be constant: as the total chlorophyll content increased (here shown as a SPAD value), the ratio Chl a/ Chl b declined significantly

6.3.2 Gas-exchange

6.3.2.1 Experiment 1

The results showed that differences in net photosynthesis rate between landraces were far less important than those due to the phenological age of the plants (Figure 6-4). There were significant differences between landraces only for the dark respiration and compensation point parameters, which describe the plants' response to light at low light intensity. No interactions between the factors were observed. The average light-response curves fitted for each group [landrace- measurement date (D1, D2)-leaf no (early leaves L1, late leaves L2)] are plotted in Figure 6-5.

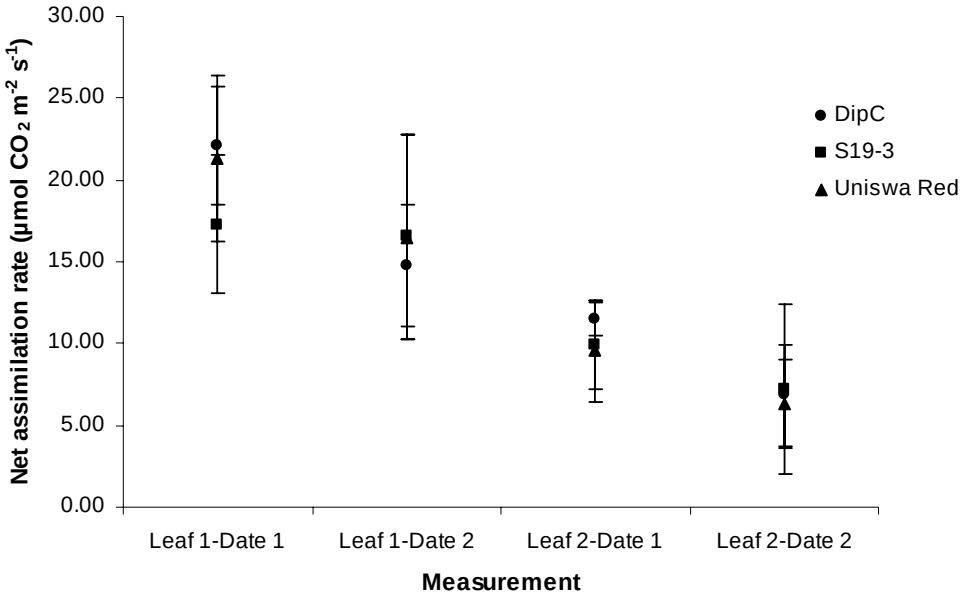

Figure 6-4: Net assimilation rate at maximum light intensity taken on two dates for early and late leaves of DipC, S19-3 and Uniswa Red, the results are an average of 8 plants, error bars are standard error of the mean.

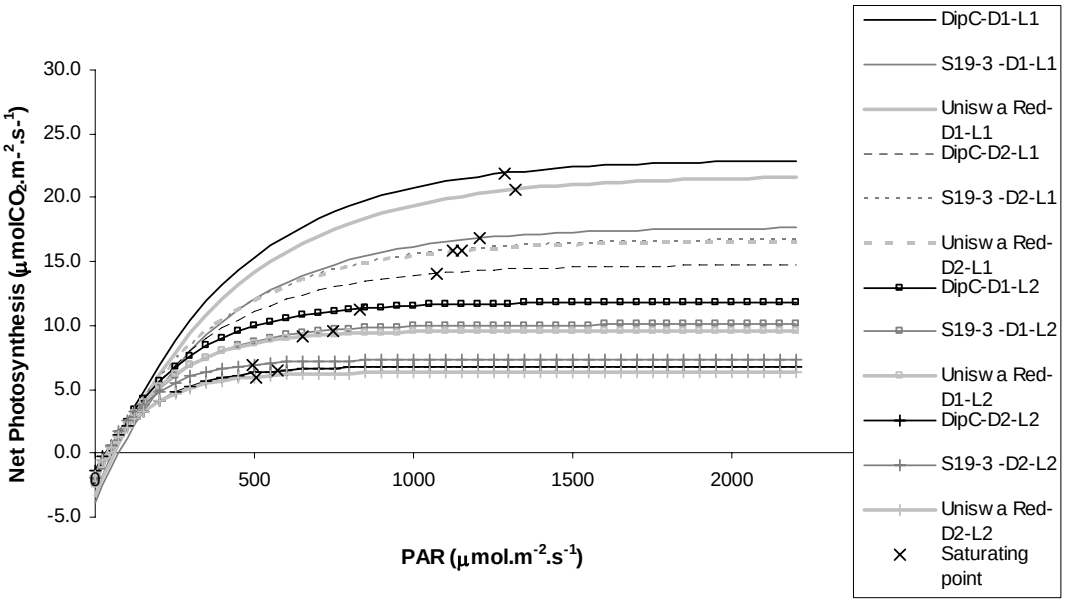

Figure 6-5: Light-response curves established with the average values of each parameter for each treatment

Table 6-1: Average parameter values for each landrace, leaf number and measuring date (± standard error of the mean), n = 8

Date	Leaf Number	Landrace	$P_{g, max}$ ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	α ($\mu mol\ CO_2\ \mu mol\ PAR)^{-1}$)	Rd ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	Ic ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)
1	1	DipC	26.4 ± 3.6	0.065 ± 0.007	3.4 ± 0.5	55.5 ± 7.3
1	1	S19-3	21.5 ± 4.6	0.057 ± 0.005	3.8 ± 1.1	79.3 ± 18.6
1	1	Uniswa Red	25.2 ± 5.8	0.060 ± 0.003	3.4 ± 0.3	60.8 ± 4.5
2	1	DipC	16.5 ± 3.7	0.050 ± 0.016	1.8 ± 0.6	39.0 ± 10.2
2	1	S19-3	18.9 ± 6.2	0.052 ± 0.013	2.1 ± 0.5	45.9 ± 16.0
2	1	Uniswa Red	19.0 ± 6.7	0.053 ± 0.016	2.4 ± 0.7	48.7 ± 9.2
1	2	DipC	14.0 ± 1.3	0.057 ± 0.015	2.2 ± 0.5	43.6 ± 9.0
1	2	S19-3	12.4 ± 3.2	0.056 ± 0.018	2.3 ± 0.8	46.7 ± 9.3
1	2	Uniswa Red	12.0 ± 3.1	0.060 ± 0.014	2.4 ± 0.9	44.6 ± 12.8
2	2	DipC	8.1 ± 3.5	0.045 ± 0.014	1.3 ± 0.5	31.6 ± 5.5
2	2	S19-3	9.2 ± 5.4	0.060 ± 0.013	1.9 ± 0.5	37.7 ± 11.1
2	2	Uniswa Red	8.1 ± 2.8	0.053 ± 0.09	1.8 ± 0.4	40.6 ± 13.8

The parameters (Table 6-1) and the light-response curves point to the following observations:

- Differences between the landraces at the same stage were difficult to detect in this experiment, and the age of the plant had more influence on the light-response curves.
- Ageing in leaves led to a reduction of the potential photosynthesis ($P_{g\ max}$) and the saturating irradiance (l_s) (i.e. the leaf's response to high light intensity), a reduction of α (efficiency of conversion of light into carbohydrates at low light intensity), and a reduction of R_d and I_c (Dark respiration and light compensation point, which determine the value of the net photosynthesis at low irradiance).
- Late-produced leaves showed lower maximum photosynthesis rate, saturating irradiance, light compensation point, and maintenance respiration (See light response curves above Figure 6-5 and Table 6-1).

Similar trends observed for photosynthetic light response curves were also found in the statistical analysis of transpiration and chlorophyll content:

- Leaf age and leaf position significantly influenced transpiration rates, whereas there was little difference between landraces of a comparable age.
- The chlorophyll concentration in a given leaf increased over time, but late-produced leaves showed lower average chlorophyll concentration.

The chlorophyll concentration in the leaf was correlated to some light-response curve parameters. A relation existed between chlorophyll content and maximum gross photosynthesis ($P_{g\ sat}$) and saturating irradiance (I_s); the correlation was highly significant ($p<0.001$) and positive: a high chlorophyll concentration improved the maximum carbon assimilation and the use of high light intensity.

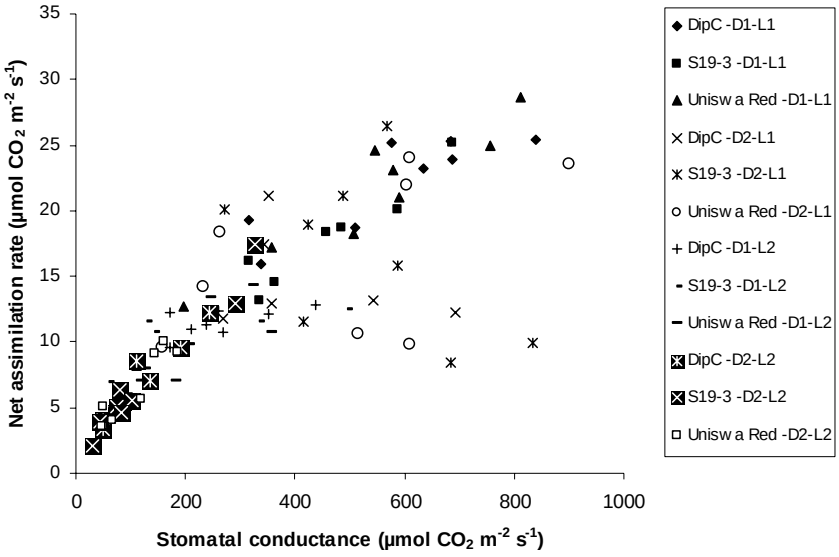

Figure 6-6: Relationship between stomatal conductance and net photosynthesis measured at saturating irradiance during the experiment 1.

Figure 6-6 shows the differences between two leaves (early and late-produced) in photosynthesis and stomatal conductance for the different landraces.

We can notice that:

- The measurements made on the first leaf at the second date (L1-D2) showed lower photosynthesis rates at similar values of stomatal conductance but with higher

variability, whereas the first-day measurements (L1-D1) for this leaf gave values following a straight line.

- The data from the second leaf (L2) shows a more linear pattern, where an increase of stomatal conductance is related to an increase of the net photosynthesis rate.

6.3.2.2 Experiment 2

The average light-response curves fitted for each group [landrace- treatment (I = irrigated, D = droughted)] at 42, 56 and 70 DAS are plotted in Figure 6-7, Figure 6-8 and Figure 6-9.

Statistical analysis of the parameters (Table 6-2) and Figure 6-7, Figure 6-8 and Figure 6-9 show that:

- there were no significant differences between the irrigated and droughted treatment for the first two sets of measurements.
- the drought effect appeared at 70 DAS, i.e. one month after the last watering in the droughted plots.
- the most evident effect is a considerable drop in the maximum net photosynthesis rate: from 24 to 10 μmol CO_2 $m^{-2}s^{-1}$ in the case of the droughted plants, whereas irrigated plants maintained their maximum photosynthesis rate.
- the value of the saturating irradiance was also reduced for droughted plants.
- the quantum yield of light (α) was lowered by the dry conditions.
- no significant landrace effect on maximum photosynthesis rate in the irrigated and droughted treatments.

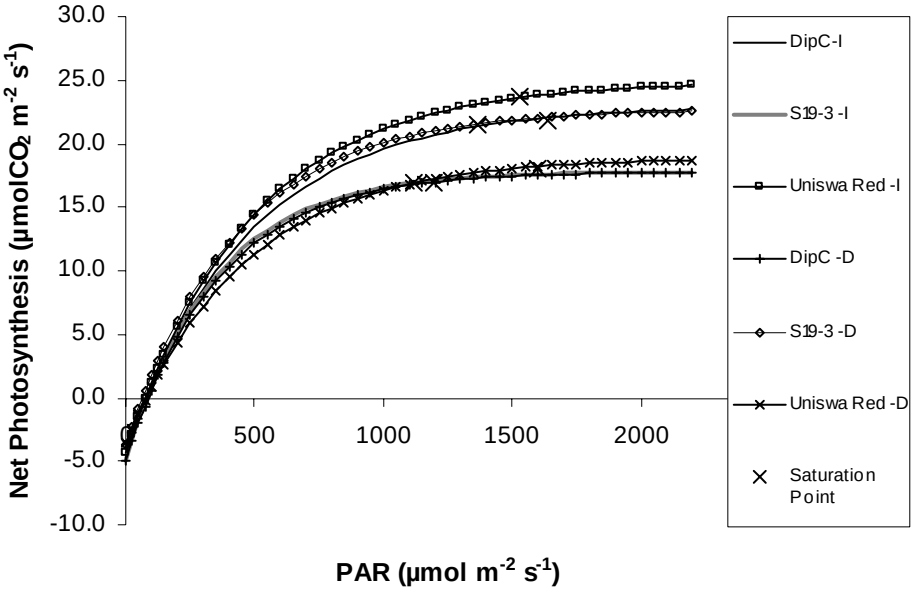

Figure 6-7: Light-response curves at 42 DAS

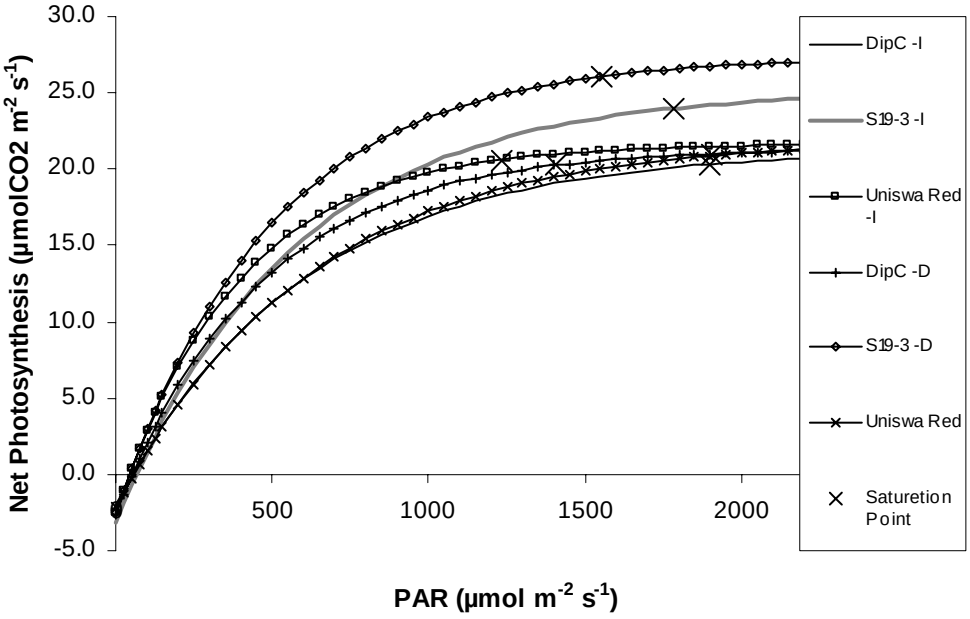

Figure 6-8: Light-response curves at 56 DAS

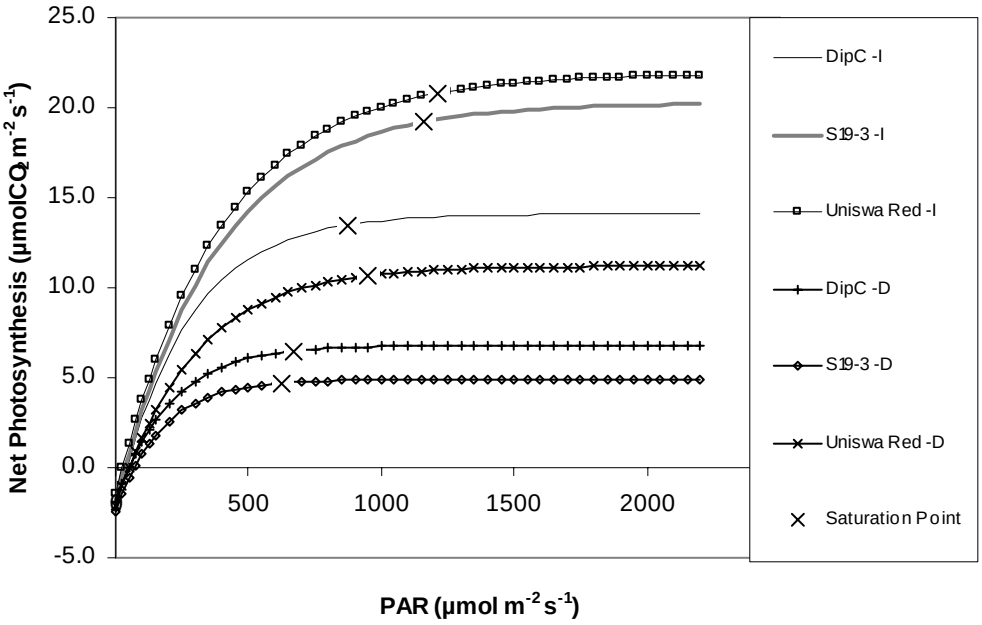

Figure 6-9: Light response curves at 70 DAS

Statistical analysis shows that there were significant differences between landraces in transpiration rates and stomatal conductance, but these differences were smaller than those brought about by water stress or the date of measurement.

In the irrigated treatment, there was little effect due to ageing, however, the landraces seemed to show different transpiration rates, with Uniswa Red transpiring more than the other two landraces see Figure 6-10.

Table 6-2: Average parameter values for each landrace, leaf number and measuring date (± standard error of the mean), n = 8

Date (DAS)	Landrace	Treatment	$P_{g, max}$ ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	α ($\mu mol\ CO_2\ \mu mol\ PAR)^{-1}$	Rd ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)
42	DipC	D	22.7 ± 3.1	0.063 ± 0.009	4.9 ± 1.8
42	DipC	I	26.8 ± 7.7	0.055 ± 0.011	3.8 ± 1.2
42	S19-3	D	26.4 ± 2.1	0.061 ± 0.002	3.7 ± 0.2
42	S19-3	I	22.7 ± 0.1	0.066 ± 0.006	4.9 ± 1.4
42	Uniswa Red	D	22.5 ± 10.1	0.049 ± 0.012	3.6 ± 1.2
42	Uniswa Red	I	29.2 ± 5.6	0.060 ± 0.003	4.3 ± 0.4
56	DipC	D	24.0 ± 9.6	0.052 ± 0.009	2.6 ± 1.0
56	DipC	I	23.3 ± 3.7	0.039 ± 0.011	2.0 ± 0.9
56	S19-3	D	29.8 ± 4.3	0.060 ± 0.009	2.5 ± 0.4
56	S19-3	I	28.3 ± 4.1	0.050 ± 0.006	3.1 ± 0.6
56	Uniswa Red	D	24.1 ± 5.8	0.039 ± 0.002	2.1 ± 0.5
56	Uniswa Red	I	24.2 ±	0.061 ± 0.004	2.5 ± 0.6
70	DipC	D	8.7 ± 1.1	0.043 ± 0.012	1.9 ± 0.4
70	DipC	I	16.5 ± 1.4	0.062 ± 0.016	2.5 ± 1.2
70	S19-3	D	7.3 ± 2.8	0.042 ± 0.014	2.4 ± 1.1
70	S19-3	I	22.2 ± 8.6	0.058 ± 0.004	1.9 ± 0.4
70	Uniswa Red	D	13.3 ± 1.3	0.045 ± 0.010	2.1 ± 0.3
70	Uniswa Red	I	23.3 ± 1.5	0.059 ± 0.002	1.4 ± 0.4

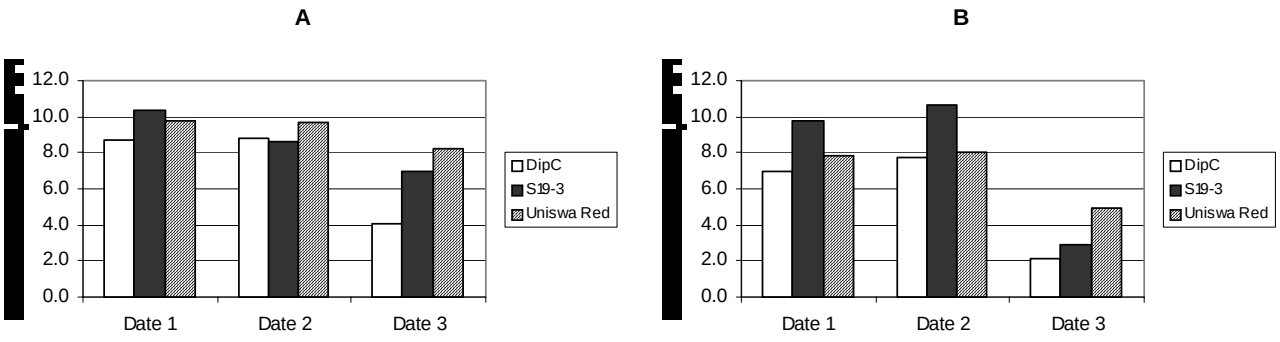

Figure 6-10: Transpiration rate for irrigated (A) and dry treatments (B)

(*n = 56, SED = 1.5*)

In the dry treatment, there was a similar effect to that observed for photosynthesis: there was a 2- to 3-fold drop in transpiration rate one month after the end of the water supplied (70 DAS) compared to the irrigated treatments.

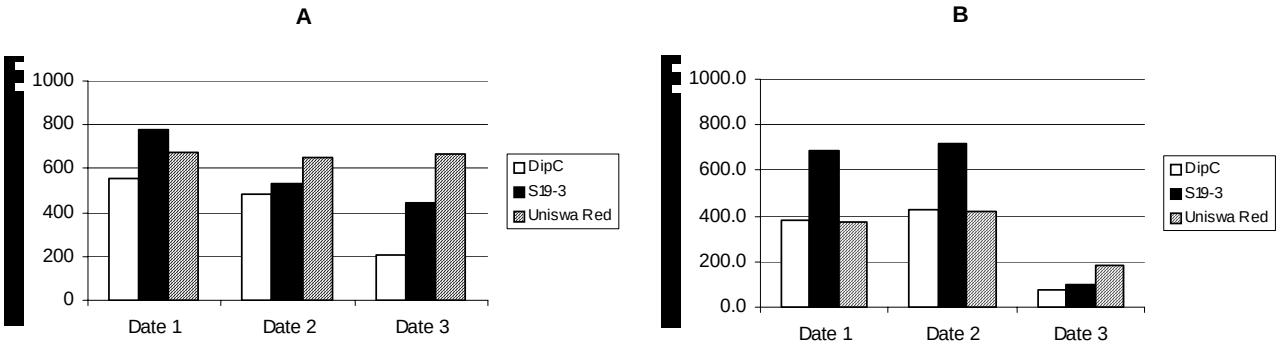

Figure 6-11: Stomatal conductance for irrigated (A) and dry treatments (B) (*n = 56, SED = 141*)

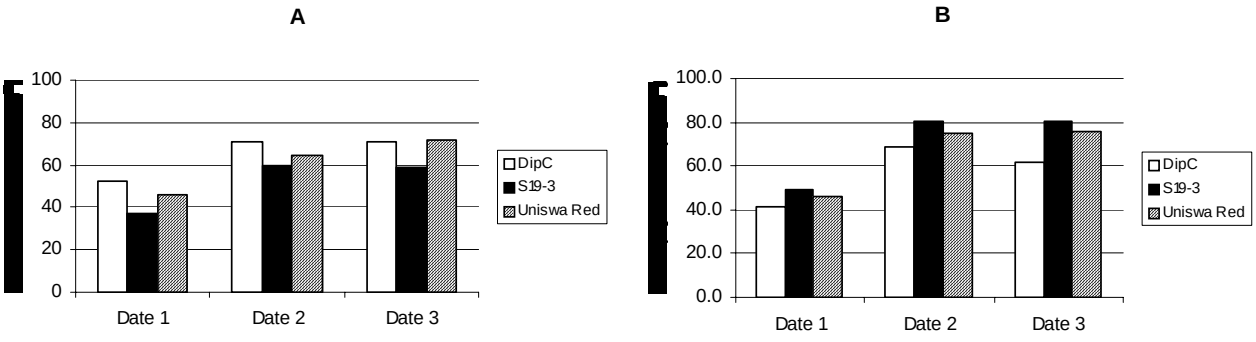

Figure 6-12: Average chlorophyll content for irrigated (A) and dry treatments (B) (*n = 56, SED = 6.3*)

Stomatal conductance was influenced by crop age and water treatment (Figure 6-11):

- Stomatal conductance remained stable in the irrigated treatment (values around 450-650 mmol m^{-2} s^{-1}), with no differences between landraces and no effect due to leaf ageing.
- The effect of drought appeared at 70 DAS, with a large reduction in stomatal conductance: from 500 to 100 mmol m^{-2} s^{-1}.
- Stomatal conductance in all of the landraces was similarly affected by drought.

The average chlorophyll content increased in the leaves over time (Figure 6-12), levelling off at two weeks after emergence.

In the irrigated treatment, S19-3 exhibited the lowest chlorophyll content, whereas DipC showed the highest.

Strong differences appeared between landraces in chlorophyll concentration depending on the water treatment: chlorophyll content in the leaves of S19-3 increased in the droughted treatment and showed then the highest chlorophyll content of the three landraces, whereas in DipC, chlorophyll content decreased and DipC showed the lowest pigment concentration; chlorophyll content in Uniswa Red was unaffected by the water treatment.

6.4 DISCUSSION

6.4.1 Chlorophyll content

The measurement of the chlorophyll content present in middle leaflets on three different landraces of bambara groundnut showed that the nature of the photosynthetic apparatus varied between these three landraces: the ratio Chl a/ Chl b is significantly different for each of these landraces. Chlorophyll a and Chlorophyll b have slightly different light absorbing patterns, resulting in absorption of different wavelengths of PAR (Lawlor, 2001).

A calibration curve was obtained relating SPAD measurements with total chlorophyll content; a linear model gives an acceptable fit (R^2 = 95%), but tends to overestimate the actual chlorophyll content in the range 20-50 SPAD units. A polynomial model gives a more accurate fit and no deviation of the residuals. Most authors however, use a linear relation because of the ease of use (Marquard and Tipton, 1987; Yadava, 1986).

During this experiment, the three landraces showed the same relationship between the SPAD values and the chlorophyll concentration, implying that the latter can be quickly estimated using a simple, non-destructive method.

6.4.2 Gas-exchange

This study -both experiments- has been made on a very small number of plants (eight plants in the case of Experiment 1, three plants during Experiment 2) and the number of measurement days was low. Despite the attempt to compare plants from a homogeneous landrace (use of seeds from a single progeny), phenological stage (same date of leaf appearance) and growing conditions, each measurement produced highly variable results. Furthermore, the plants grown in Experiment 1 seem to have encountered unfavourable conditions beyond our control. For example, the light intensity received by the plants between measurements was low because of the time of year (March/April). The temperature during the afternoon regularly exceeded the optimum values published for this species, because of problems with the vents of the glasshouse compartment. The plants were also severely affected by an infestation of red spider mites (*Tetranycus urticae*).

Despite these limitations, the present study on the gas-exchange parameters of bambara groundnut gave some preliminary indications about the species' characteristics, the variability between and within landraces, and the response to environmental and phenological factors.

The values of the different gas-exchange parameters (Singleton-Jones, 1998; Valle *et al*., 1985) and their response to drought (Clifford *et al*., 2000) are similar to other C_3

species. What is even more important is that the results do not show any differences between the landraces at comparable ages with respect to their photosynthetic potential. This is particularly important, as it indicates that photosynthetic behavior is a species trait and not determined by landrace.

Many crop models will need to use a value for the radiation use efficiency (e_r, see Chapter 3) in order to give an accurate prediction of the growth and productivity of plants. Literature suggests a value of 1.2 g MJ^{-1} (Azam-Ali *et al*., 2001) for bambara groundnut. A value for the e_r under glasshouse conditions can be calculated by using a simple model and the data presented above. This model is based on the assumptions that light travels through the crop following Beer's law (Azam-Ali and Squire, 2002) and uses the values of the light response curves.

6.5 CONCLUSIONS

In these two experiments, the plants were grown in slightly different conditions (as discussed above). Nevertheless, some results can be found in common in the two experiments:

1. The different landraces didn't show different photosynthetic potentials in terms of maximum net photosynthesis rate, quantum yield and saturating irradiance. The transpiration rate in absence of water shortage, was similar for the three landraces.
2. There was a logarithmic-shaped relationship between photosynthesis rate and stomatal conductance, suggesting that at higher stomatal conductance values, other factors become more important in limiting photosynthesis rate.

On the other hand, the two experiments gave some contradictory results:

1. The leaf ageing effect observed in Experiment 1 was not observed in Experiment 2; the cause of such a difference can be possibly found in the differences in growing conditions, especially the presence of parasites (red spider mites) in Experiment 1, could have accelerated the leaf senecense.

2. Differences in transpiration between landraces appeared to be significant in Experiment 1, but not in Experiment 2; this difference originated from the interaction between landrace and water shortage.

SPAD measurements can be used for a fast and non destructive measurement of chlorophyll content of the leaves.

CHAPTER 7 MODEL DEVELOPMENT: BIOMASS PRODUCTION AND YIELD FORMATION

The following paragraphs describe how the biomass production and yield formation are calculated in the BamGro model. As seen in Chapter 4, development can be described in terms of a vegetative phase (emergence, leaf production, leaf area growth, total dry matter production and dry matter distribution) and a reproductive phase (flower production and pod formation and total yield). Unlike cereal crops, in bambara groundnut there is a certain overlap of these phases in that leaf production continues even after flowering and podding have started. To model this, we have therefore assumed that crop development is under the control of two independent 'clocks'. One influences a continuous leaf production and consequently leaf area production, while the other influences the biomass distribution as affected by reproductive processes. As these processes run parallel one clock would not be sufficient.

7.1 WATER AVAILABILITY

As no data were available on soil water content in the experiments used to determine the soil-water relations for BamGro, it was decided to use the water routine of the PALM model (Matthews, 2005) upon which BamGro is based.

BamGro divides the top one meter of the soil in four zones. It calculates the ratio between water supply and potential transpiration. The water supply component is influenced by the actual water content of the soil layers and the depth and distribution of the root sytem.

BamGro calculates two multipliers between zero and one, depending on the relation between water supply (based on rainfall, initial water content and water release factors and the rooting depth of the plant) and potential transpiration. One multiplier affects the

biomass production (WM_1), while the other affects the leaf appearance rate and rate of expansion in leaf area (WM_2).

Biomass production is insensitive to water stress until a critical value is reached and thereafter decreases linearly. Leaf appearance rate and leaf expansion rate decrease linearly over the whole range, based on the relation between water supply and potential transpiration.

Based on observations in the glasshouse experiments phenology is assumed to be unaffected by drought.

7.2 EMERGENCE

Bambara groundnut has an extrapolated theoretical base temperature of 9.9 ^{0}C for germination (Kocabas *et al*. 1999). In practice, there is no germination below 12 ^{0}C and above 45 ^{0}C (Kocabas *et al*. 1999; Massawe, 2002). The germination rate has an optimum temperature of 32.3 °C (Kocabas *et al.* 1999). BamGro assumes a base temperature of 9.9 °C for all developmental events.

The time between sowing and germination varies between the different landraces and usually is between 5 and 9 phenochrons (see Table 7-1).

Table 7-1: Interval between sowing and emergence for 12 bambara groundnut landraces (values based on Swaziland field data, except ▲ based on TCRU glasshouse experiments).

Landrace	Base temp (^{0}C)	Time to emergence (Phenochrons)
GabC	9.9	5
DipC	9.9	6
OM1	9.9	6
AHM753	9.9	6
AHM968	9.9	5
AS17	9.9	6
Nyakeni C1	9.9	5
Nyakeni C2	9.9	5
UniswaRed	9.9	6
S19-3*▲	9.9	9
Uniswa Red▲	9.9	6
DipC▲	9.9	6

*Not in field experiment ▲Adjusted for glasshouse

7.3 DRY MATTER PRODUCTION

Daily drymatter production is calculated based upon an empirical equation (see Chapter 4) calculating the increase in biomass per unit of intercepted radiation, using e_r, PAR, L and plant density.

$$DM = S_{total} \times PAR \times e_r \left(1 - e^{-kL}\right) \times pd$$

where:

DM: Total drymatter (g m^{-2} d^{-1})

S_{total}: Daily Radiation (MJ m^{-2} d^{-1})

PAR: Photosynthetically Active Radiation[2]

e_r: Radiation Use Efficiency (g MJ^{-1})

k: Extinction coefficient

LAI: Leaf Area Index (m^2 leaf m^{-2} ground)

pd: Plant density (plants m^{-2})

BamGro assumes a PAR of 0.5 and and e_r of 2.4 g MJ^{-1} (Azam-Ali *et al*., 2001).

In case of drought the DM is corrected, as described in the water availability section:

$$DM_w = DM \times WM_1$$

where:

DM_w: Total drymatter (g m^{-2} d^{-1}) under water stress

DM: Total drymatter (g m^{-2} d^{-1})

WM_1: Multiplier for water stress, effecting drymatter production

7.4 LEAF NUMBER

Figure 7-1 shows the relation between number of leaves and phenological age. From this relation the phyllochron can be determined. This is the number of phenochrons between two successive leaves, represented by the slope of the relation. For modelling purposes this relation is divided into two linear relationships. The number of leaves increases until a maximum number (line A), after which no increase in leaf number is

[2] Radiation within the visible range (0.4 – 0.7 μm) (Azam-Ali and Squire, 2002)

observed (Line B). Line B is an equilibrium between new leaves being produced continuously and old ones dying through senescence.

When the plant is under stress or is very late maturing, a third phase can be observed, in which the number of leaves declines rapidly (Line C). Although the shape of the relation is similar for the landraces, the maximum leaf number and the slope of line A differs for each landrace.

The total number of leaves per plant per total accumulated phenochrons (N_l, number of leaves plant^{-1}) is calculated as:

$$N_l = pi \times N_{ph}$$

where:

N_l: Total number of leaves (plant^{-1})

pi: Phyllochron (number of leaves plant^{-1} (phenochron)$^{-1}$)

N_{ph}: Number of accumulated phenochrons (phenochron)

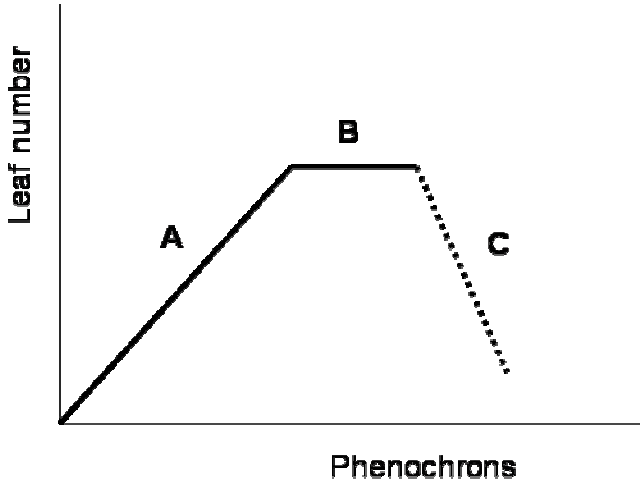

Figure 7-1: Simplified relationship between leaf number per plant and phenological age as used by BamGro

Table 7-2: Landrace specific parameters used for the calculation of leaf appearance (values based on Swaziland field data, except ▲ based on TCRU glasshouse experiments). Values are een average of 3 years for the field data and an average of 4 years for the glasshouse data (± standard error of the mean).

Landrace	**Phyllochron** (no. leaves plant^{-1} (phenochron)$^{-1}$)		
GabC	0.32	±	0.03
DipC	0.34	±	0.02
OM1	0.31	±	0.01
AHM753	0.34	±	0.02
AHM968	0.30	±	0.02
AS17	0.33	±	0.03
Nyakeni C1	0.34	±	0.01
Nyakeni C2	0.34	±	0.03
UniswaRed	0.35	±	0.01
S19-3*▲	1.18	±	0.23
Uniswa Red▲	0.99	±	0.30
DipC▲	1.06	±	0.10

*Not in field experiment ▲Adjusted for glasshouse

Values of the phyllochron, represented by the slope of line A, as used by the model can be found in Table 7-2.

7.5 LEAF AREA

BamGro calculates the rate of increase of leaf area per plant per phenochron as a function of the current leaf number (as calculated in the previous section) using a linear fitted relation:

$$RIL = \kappa(N_l) + \lambda$$

where:

RIL: Rate of increase in leaf area (cm^2 phenochron^{-1} (plant)$^{-1}$)

N_l: current leaf number (plant $^{-1}$)

κ: Landrace specific parameter (cm^2 plant^{-1})

λ: Landrace specific parameter (cm^2 phenochron^{-1} (plant)$^{-1}$)

The values for α and β used by BamGro can be found in Table 7-3.

Table 7-3: Landrace specific parameters used for the calculation of leaf area and R^2 of the fitted relation (values based on Swaziland field data, except ▲ based on TCRU glasshouse experiments).

Landrace	**κ** (cm^2 plant^{-1})	**λ** (cm^2 phenochron^{-1} (plant)$^{-1}$)	**R^2**
GabC	0.25	26.2	0.911
DipC	0.26	29.9	0.933
OM1	0.19	29.8	0.876
AHM753	0.29	23.1	0.897
AHM968	0.18	25.4	0.877
AS17	0.32	26.9	0.922
Nyakeni C1	0.29	26.8	0.884
Nyakeni C2	0.31	21.7	0.878
UniswaRed	0.25	24.4	0.854
S19-3*▲	0.82	23.3	0.838
Uniswa Red▲	0.39	22.5	0.867
DipC▲	0.48	21.4	0.872

*Not in field experiment ▲Adjusted for glasshouse

For every day BamGro calculates the number of phenochrons and updates the value of the leaf area state variable by the value of RIL. This leaf area per plant value is

converted into a per area value (i.e. Leaf Area Index, LAI) by multiplying it by the number of plants per square metre.
In case of drought the RIL is corrected, as described in the water availability section:

$$RIL_w = RIL \times WM_2$$

where:

RIL_w: Rate of increase in leaf area (cm^2 $phenochron^{-1}$ $(plant)^{-1}$) under water stress

RIL: Rate of increase in leaf area (cm^2 $phenochron^{-1}$ $(plant)^{-1}$)

WM_2: Multiplier for water stress, effecting leaf area expansion

7.6 BIOMASS DISTRIBUTION

Each day, BamGro calculates how the total dry matter as calculated above is allocated to each plant component (leaves, stem, roots, and pods (when present). The rules by which this is done depend on the stage the crop is in.

7.6.1 Vegetative and Flowering phase

During the vegetative and flowering stages, the crop distributes its dry matter between leaves (LW), stems and petioles (SW) and roots (RW). Values for the Specific Leaf Area (the leaf area per unit leaf weight) can be found in Table 7-4.

Leaf weight per plant:

$$LW = \frac{LA}{SLA}$$

where:

LW: Weight of leaves (g plant^{-1})

LA: Leaf area (cm^2 plant^{-1})

SLA: Specific Leaf Area (cm^2 g^{-1})

Shoot weight:

$$SW = LW \times pc$$

where:

LW: Weight of leaves (g plant^{-1})

SW: Weight of stems and petioles (g plant^{-1})

pc: Partitioning coefficient

BamGro uses a pc of 0.2 during the vegetative stage, 0.3 during the flowering stage and 0.8 during the podding stage. These values are based on the relation between leaf weight and the weight of stems and petioles of bambara groundnut in the field in Swaziland (Sesay *et al*., 2003b).

Root weight

$$RW = DM - (LW + SW)$$

where:

RW: Weight of roots (g plant^{-1})

LW: Weight of leaves (g plant^{-1})

SW: Weight of stems and petioles (g plant^{-1})

DM: Total drymatter (g plant^{-1})

When the weight of leaves and the weight of stems and petioles equal or exceed the total drymatter produced, the relation is corrected, so the roots always receive at least 20% of the total drymatter and there are no negative growth rates.

Table 7-4: Landrace dependent specific leaf area (values based on Swaziland field data, except ▲ based on TCRU glasshouse experiments). Values are een average of 8 measurements for the field data and an average of 40 measurements for the glasshouse data (± standard error of the mean).

Landrace	SLA ($cm^2\ g^{-1}$)		
GabC	270	±	29
DipC	285	±	47
OM1	289	±	33
AHM753	299	±	44
AHM968	316	±	49
AS17	284	±	59
Nyakeni C1	267	±	36
Nyakeni C2	262	±	39
UniswaRed	235	±	34
S19-3*▲	170	±	26
Uniswa Red▲	177	±	21
DipC▲	176	±	27

*Not in field experiment ▲Adjusted for glasshouse

7.6.2 Pod filling phase

During the pod filling stage the crop distributes its dry matter between leaves (LW), stems and petioles (SW), roots (RW) and pods (PW).

SW and LW are calculated as in the vegetative and flowering phase. BamGro gives preference to PW over SW, RW and LW in the podfilling stage.

BamGro uses a landrace-specific linear relation to calculate the rate of increase in the weight of the pods, when the podding stage is reached:

$$PW = P_{con} \times N_{ph}$$

where:

PW: Weight of pods (g plant^{-1})

P_{con}: Weight increase constant for pods (g phenochron^{-1} (plant)$^{-1}$)

N_{ph}: number of phenochrons (phenochron)

Table 7-5: Weight increase constant for pods, R^2 of the fitted relation and interval between onset of flowering and onset of podding for 12 bambara groundnut landraces (values based on Swaziland field data, except ▲ based on TCRU glasshouse experiments).

Landrace	P_{con} (g phenochron^{-1} (plant)$^{-1}$)	R^2	Time to podding (Phenochrons)
GabC	0.93	0.756	17
DipC	0.86	0.753	16
OM1	0.92	0.601	16
AHM753	0.96	0.765	16
AHM968	0.62	0.695	16
AS17	0.97	0.851	17
Nyakeni C1	1.21	0.857	16
Nyakeni C2	1.06	0.835	18
UniswaRed	1.08	0.800	16
S19-3*▲	0.92	0.780	16
Uniswa Red▲	1.08	0.800	16
DipC▲	0.86	0.753	16

*Not in field experiment ▲Adjusted for glasshouse

P_{con} is calculated from the fitted relation between pod weight and phenological age (Figure 7-2). P_{con} is the weight increase per phenochron, represented by the slope of the relation.

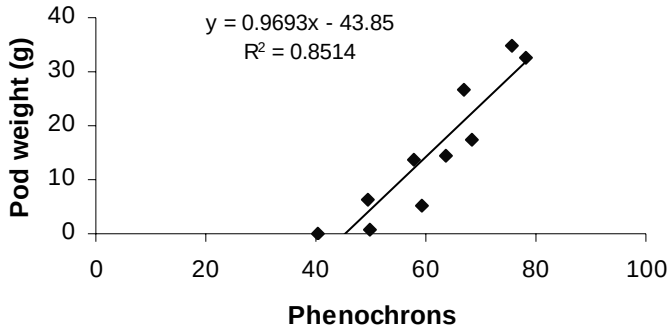

Figure 7-2: Fitted relationship between pod weight per plant and phenological age for AS17, grown at the Malkerns field site, Swaziland.

During the pod filling phase root weight is calculated as:

$$RW = DM - (LW + SW + PW)$$

where:

RW: Weight of roots (g plant^{-1})

DM: Total drymatter (g plant^{-1})

LW: Weight of leaves (g plant^{-1})

SW: Weight of stems and petioles (g plant^{-1})

PW: Weight of pods (g plant^{-1})

7.7 PHOTOPERIOD EFFECT

In most bambara groundnut landraces, both flowering and the onset of pod filling are influenced by photoperiod All the landraces used in the field and glasshouse experiments are photoperiod-sensitive for pod filling. Unfortunately, the photoperiod sensitivity of these landraces has not been quantified as a single photoperiod treatment (12h) is routinely imposed on all landraces in the TCRU glasshouses.

BamGro uses a very simplified representation of the photoperiod sensitivity of all landraces. Bambara groundnut is a short day plant. BamGro assumes that there is no effect of daylength on pod filling when the daylength is less than 12 h and that pod filling does not take place when the photoperiod is more than 18 h (Brink, 1997; Linnemann and Craufurd, 1994).

Allthough the degree of photoperiod-sensitivity is a genetic trait, BamGro assumes that daylength influences all landraces in the same way, because the photoperiod effect has not been quantified for the landraces used in this project. It does, however, take basic photoperiod restrictions into account, preventing the prediction of bambara groundnut yield formation in areas or seasons that have long days.

BamGro calculates a multiplier when the photoperiod is longer then 12 h. This multiplier is used to slow down the advancement of the podfilling stage, preventing the formation of yield. The multiplier decreases linearly between 12 and 18 h (see also Figure 4-6, Chapter 4).

7.8 FLOWERING

The time to first flowering differs per landrace and per environmental circumstances. The number of phenochrons to first flowering (calculated as the number of phenochrons and 50% of the crop flowering) used by the model for a number of landraces are shown in Table 7-6.

Table 7-6: Appearance constant for flowering, R^2 of the fitted relation and interval between emergence and flowering for 12 bambara groundnut landraces (values based on Swaziland field data, except ▲ based on TCRU glasshouse experiments)

Landrace	F_{con} (no. of flowers phenochron^{-1})	R^2	Time to flowering (Phenochrons)
GabC	2.13	0.959	25
DipC	2.65	0.973	23
OM1	2.46	0.953	24
AHM753	2.47	0.968	24
AHM968	2.86	0.949	24
AS17	2.36	0.968	24
Nyakeni C1	2.53	0.955	25
Nyakeni C2	2.57	0.964	24
UniswaRed	2.44	0.960	24
S19-3*▲	0.80	0.872	24
Uniswa Red▲	1.18	0.987	24
DipC▲	1.15	0.932	23

*Not in field experiment ▲Adjusted for glasshouse

Flowers are normally carried in pairs, on short penduncles, which arise in the axils formed by the petioles and the stem (Doku, 1968; Linnemann, 1994). The upper limit for the flower production can, therefore, be estimated by the following relation:

$$Fpot = 2 \times N_l$$

where:

Fpot: Potential number of flowers (plant^{-1})

N_l: Number of leaves (plant^{-1})

When the flowering phase is reached, BamGro uses a landrace-specific linear relation to calculate the rate of appearance of the flowers, below the upper limit, when the flowering stage is reached:

$$F_{act} = F_{con} \times N_{ph}$$

where:

F_{act}: Actual number of flowers (plant^{-1})

F_{con}: Appearance constant for flowering (no. of flowers phenochron^{-1}), see Table 7-6.

N_{ph}: number of phenochrons since the start of the flowering phase

F_{con} is calculated from the fitted relation between average accumulative number of flowers and phenological age (Figure 7-3). F_{con} is the number of flowers per phenochron, represented by the slope of the relation

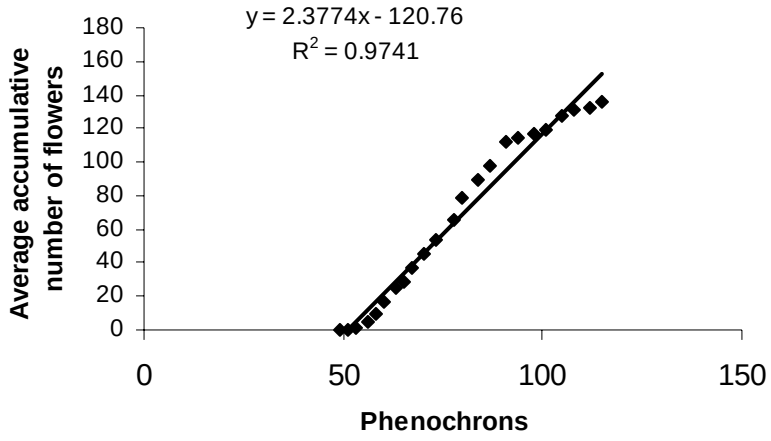

Figure 7-3: Fitted relationship between average accumulative number of flowers per plant and phenological age for GabC, grown at the Malkerns field site, Swaziland (2002).

7.9 MATURITY

Table 7-7: Interval between podding and physiological maturity for 12 bambara groundnut landraces (values based on Swaziland field data, except ▲ based on TCRU glasshouse experiments)

Landrace	Time to maturity (Phenochrons)
GabC	29
DipC	27
OM1	27
AHM753	27
AHM968	30
AS17	27
Nyakeni C1	28
Nyakeni C2	28
UniswaRed	30
S19-3*▲	39
Uniswa Red▲°	43
DipC▲	42

*Not in field experiment ▲Adjusted for glasshouse

7.10 MODEL INPUTS

7.10.1 Input file

BamGro uses a standardised text file as an input to the model. This file contains a specific code for the landrace used in the simulation. Further more it contains the parameters relating to the simulation controls (simulation dates, reference to weather file), information on crop management (the sowing date, plant spacing) and information

on soil characteristics (bulk density, sand fraction, silt fraction, initial soil moisture content and water release parameters) of the site.

7.10.2 Parameter file

BamGro uses a parameter file containing the model parameters for each specific landrace. It is an Excel file, in which the columns represent the different parameters, and the rows the different landraces. These parameters are accessed by a routine which takes the crop species and landrace identifier as arguments, and returns the parameter identifiers and their values as a string which can then be used by the model when instructed.

7.10.3 Weather data

BamGro needs weather data on a daily time step to run (maximum and minimum temperature, rainfall and solar radiation). Data has been used from two different sources:

1. Actual recorded data
2. Data simulated by a weather generator

The data is read into the model using a text file in standard DSSAT format (Uehara and Tsuji, 1993).

In Swaziland, maximum temperature, minimum temperature and rainfall were recorded for both Malkerns and Luve. Sunshine hours were only available for Malkerns. For the simulations at Luve radiation has been simulated with a weather generator (see below).

7.10.3.1 Conversion of sunshine hours into radiation

Solar radiation data (MJ m^{-2} d^{-1}) was not available for any of the field sites. However, solar radiation can be estimated using the Ångström equation (Ångström, 1924; Collinson, 1996):

$$Rs = Ra\left(a1 + a2 \times \frac{n}{N}\right)$$

where Ra is the extra-terrestrial radiation or Angot value, a1 and a2 are site specific Ångström coefficients, n is the recorded number of sunshine hours and N is the site specific maximum sunshine hours. In this study a value of 0.25 has been used for a1 and a value of 0.5 has been used for a2 to estimate the solar radiation for the field sites.

7.10.3.2 Weather generator

A problem with the available sets of weather data is that they are not complete. Due to this technical problem, gaps of missing data of a month or more during the growing season of the crop are not uncommon. For periods of missing data up to 10 days, BamGro is able to use interpolated values, but for more than ten days of missing weather data a solution had to be found. Furthermore, for predictions, BamGro needs daily weather data for long periods of time.

In order to overcome this problem the MarkSim weather generator (Jones and Thornton, 2000) was used. The software is capable to generate weather for any grid point in Africa.

This program is based on a stochastic weather generator that uses a third order Markov process to model daily weather data. The model has been fitted to more than 9200 stations with long runs of daily data throughout the world (Jones and Thornton, 2000). The climate normals for these stations were assembled into 664 groups using a

clustering algorithm. For each of these groups, rainfall model parameters are predicted from monthly means of rainfall, air temperature, diurnal temperature range and station elevation and latitude. The program identifies the cluster relevant to any required point using interpolated climate surfaces at a resolution of 18 km^2 and evaluates the model parameters parameters for that point (Jones and Thornton, 2000).

MarkSim has been used to generate data to fill up the gaps in the existing data and to generate full data sets for future predictions. Predicted weather has been compared to observed rainfall and temperature. A basic statistic test (ANOVA, $p < 0.05$) found no difference between observed and predicted values.

7.10.4 Schematic overview of the dataflow through the model

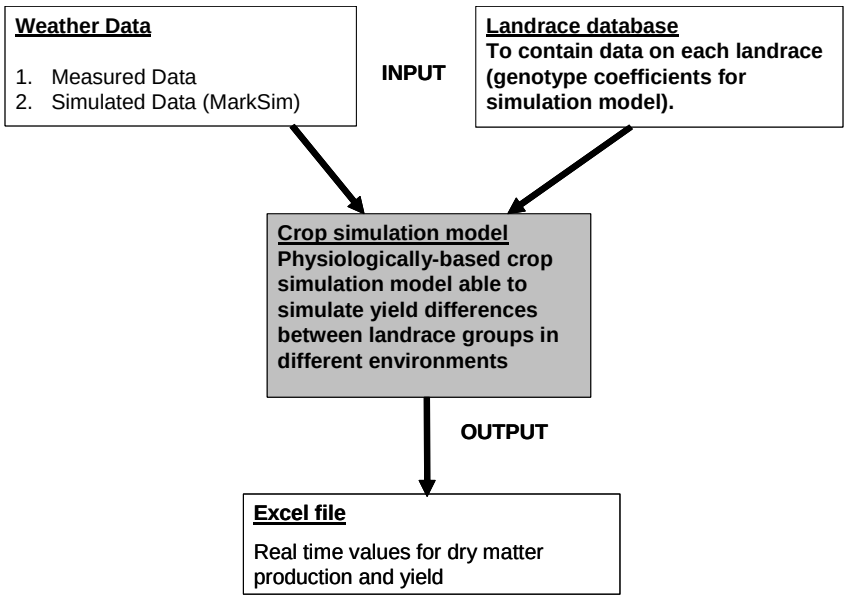

Figure 7-4: Schematic overview of the dataflow through the model

CHAPTER 8 MODEL DEVELOPMENT: VALIDATION

8.1 INTRODUCTION

BamGro was validated against three independent sets of data. These were:

1) TCRU glasshouses (2003 season)
2) Swaziland 'Malkerns' field site (2002-2003 season)
3) Swaziland 'Luve' field site (2002-2003 season).

The Malkerns field data is used to evaluate the model performance in a non limiting environment. Allthough the crop is rainfed and no additional irrigation is applied, the crop does not run out of water during the growing season. Furthermore, fertilizer is applied at sowing of the crop ensuring that the crop has an adequate supply of nutrients during its lifecycle. Insecticide and fungicide are applied at regular intervals to protect the crop.

The Luve field data has been included to evaluate the performance of the water routine of the model and the effect of drought on the predictions.

Due to the large differences between glasshouse grown landraces and field grown landraces (see Chapter 4), only glasshouse grown landraces are validated against glasshouse data and only field grown landraces are validated against field data (glasshouse landraces have adjusted leaf area parameters, phyllochron interval, SLA, podding constant and time to maturity, see Chapter 7). In Table 8-1 the starting values of each validation can be found.

Table 8-1: Overview of the number of landraces validated and validation starting values

	Glasshouse	Field Malkerns	Field Luve
Number of landraces	3	9	3
Simulation start	28/04/2003	25/11/2002	09/12/2002
Simulation end	30/10/2003	30/05/2003	30/05/2003
Soil type	sandy loam	sandy loam	sand
Initial soil water content	0.28 m^3 H_2O m^{-3} soil	0.28 m^3 H_2O m^{-3} soil	0.0 m^3 H_2O m^{-3} soil

The landraces used in the glasshouse were : Uniswa Red, DipC and S19-3. For the Malkerns field site validation OM1, GabC, DipC, AHM968, AHM753, AS17, NyakeniC1, NyakeniC2 and Uniswa Red were used. Three landraces were tested for the Luve field site. These were: Uniswa Red, OM1 and AS17.

Weather files have been constructed for each validation site. The amount of rain/irrigation and minimum and maximum temperature has been measured for each site. The input radiation has been measured for the glasshouse and estimated from sunshine hours for Malkerns field data when sunshine hours were available. The gaps in the radiation data for the field sites and all solar radiation for Luve have been generated using the MarkSim software.

8.2 RESULTS OF THE VALIDATION

8.2.1 Glasshouse data

Figure 8-1 shows the model performance for predicting total above ground biomass in the glasshouse experiment.

The model clearly underestimates the total above ground biomass for each landrace by about 50%, however the general shape of the predicting curve is similar to that observed in the glasshouse. There is a very strong correlation between the observed and simulated total above ground biomass for all three landraces.

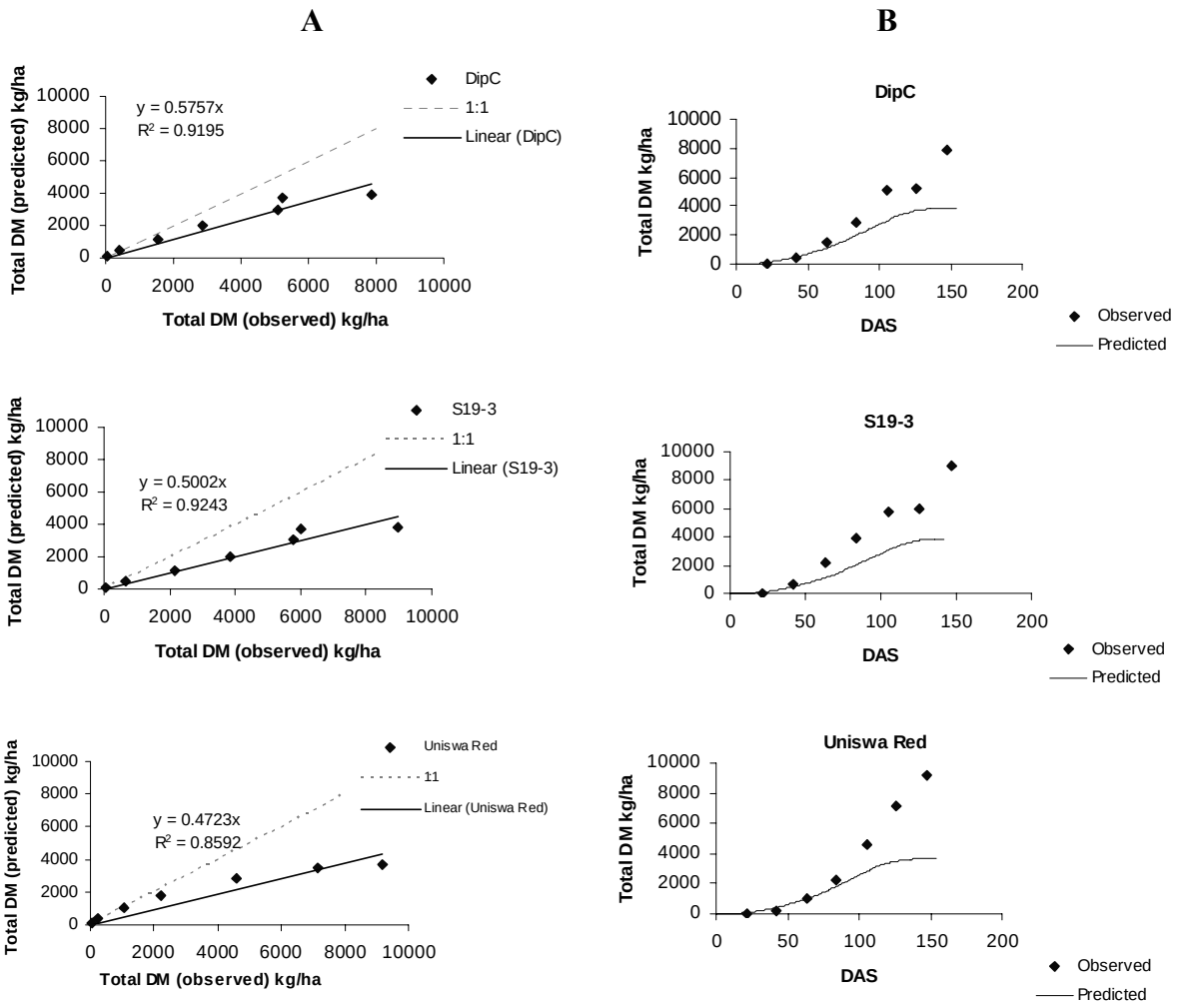

Figure 8-1: Relationship between observed and predicted total above ground biomass (Total DM kg ha^{-1}) (A) and the relationship between observed and predicted above ground biomass (Total DM kg ha^{-1}) with time (Days After Sowing; DAS) for DipC, S19-3 and Uniswa Red (B) grown in the TCRU glasshouses.

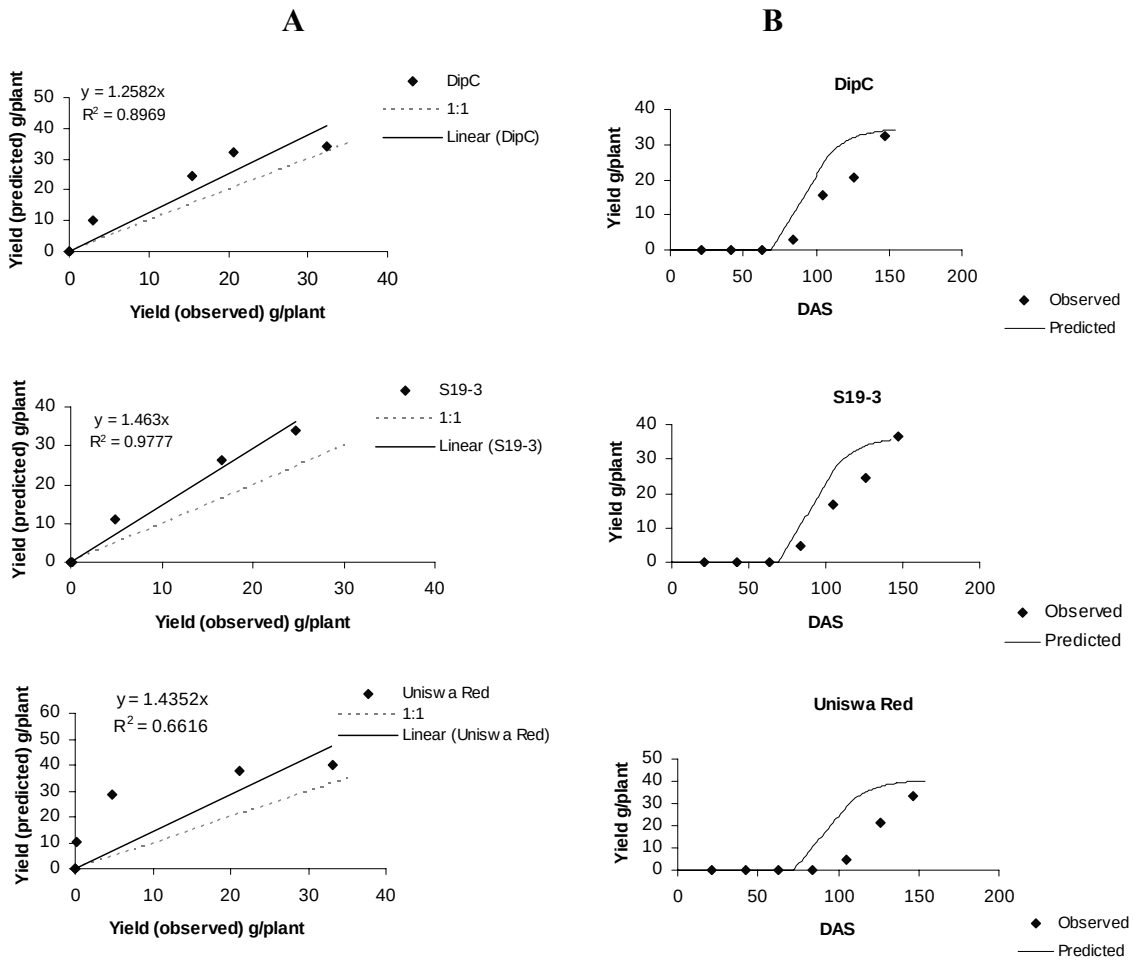

Figure 8-2: Relationship between observed and predicted pod yield per plant (g plant^{-1}) (A) and the relationship between observed and predicted pod yield per plant (g plant^{-1}) with time (Days After Sowing; DAS) for DipC, S19-3 and Uniswa Red (B) grown in the TCRU glasshouses.

The model overestimates the pod yield during the beginning of the pod filling phase for each landrace (Figure 8-2). However, the model does estimate the final pod yield accurately, due to a significant slowing down of the increase in predicted pod weight. There is a strong correlation between the observed and predicted pod yields for DipC and S19-3. The model performs least well for Uniswa Red, where it overestimates the pod yield over the whole pod filling stage and the correlation between observed and estimated pod yields is weakest (R^2=0.66).

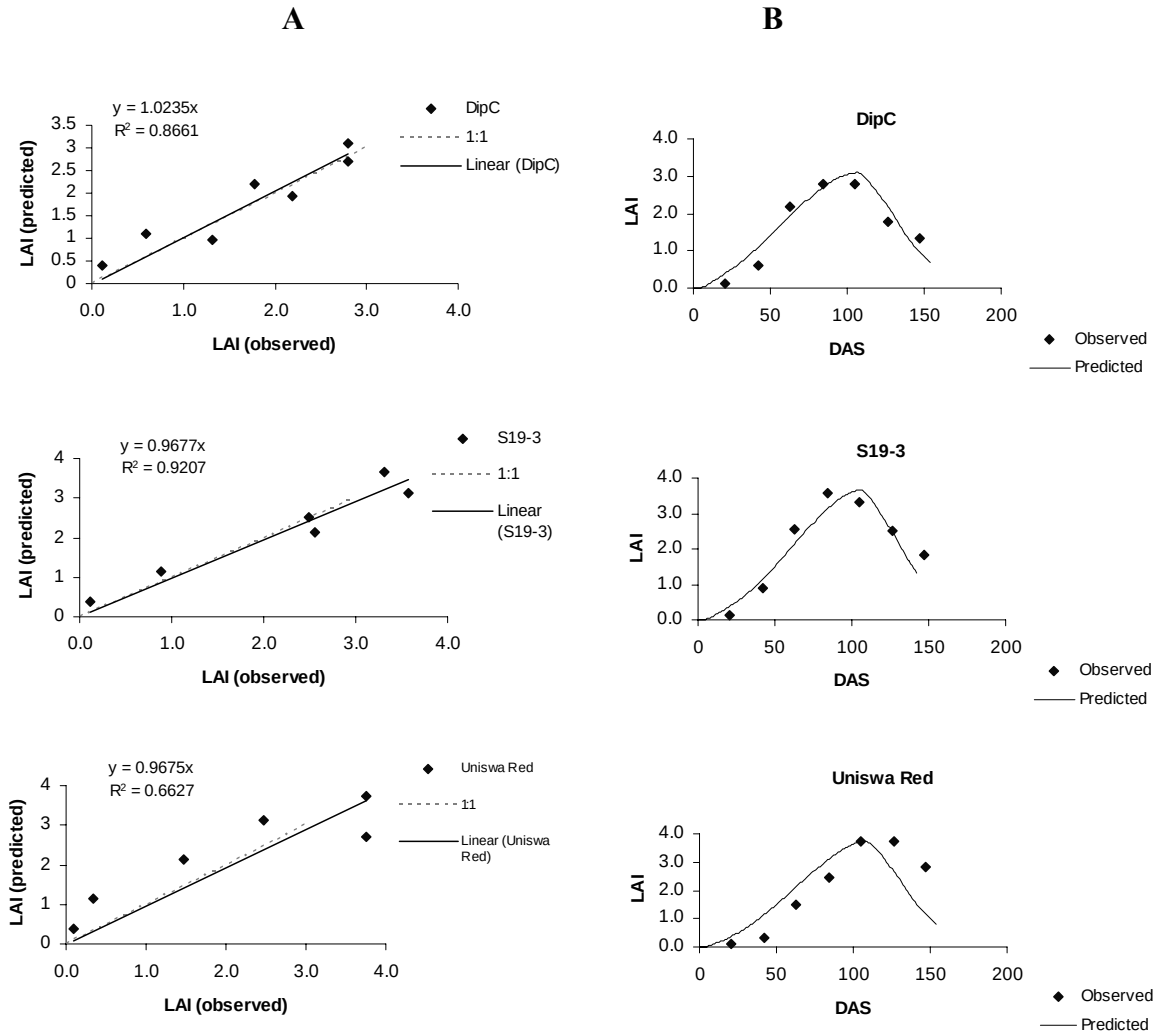

Figure 8-3: Relationship between observed and predicted Leaf Area Index (A) and the relationship between observed and predicted Leaf Area Index with time (Days After Sowing, DAS) for DipC, S19-3 and Uniswa Red (B) grown in the TCRU glasshouses.

The model achieves an excellent fit between observed and predicted LAI for DipC and S19-3 (Figure 8-3). There is a very strong correlation between the observed and predicted LAI for DipC and S19-3. Although less than the other landraces, the model still achieves a good fit between observed and predicted LAI for Uniswa Red.

8.2.2 Malkerns Field data

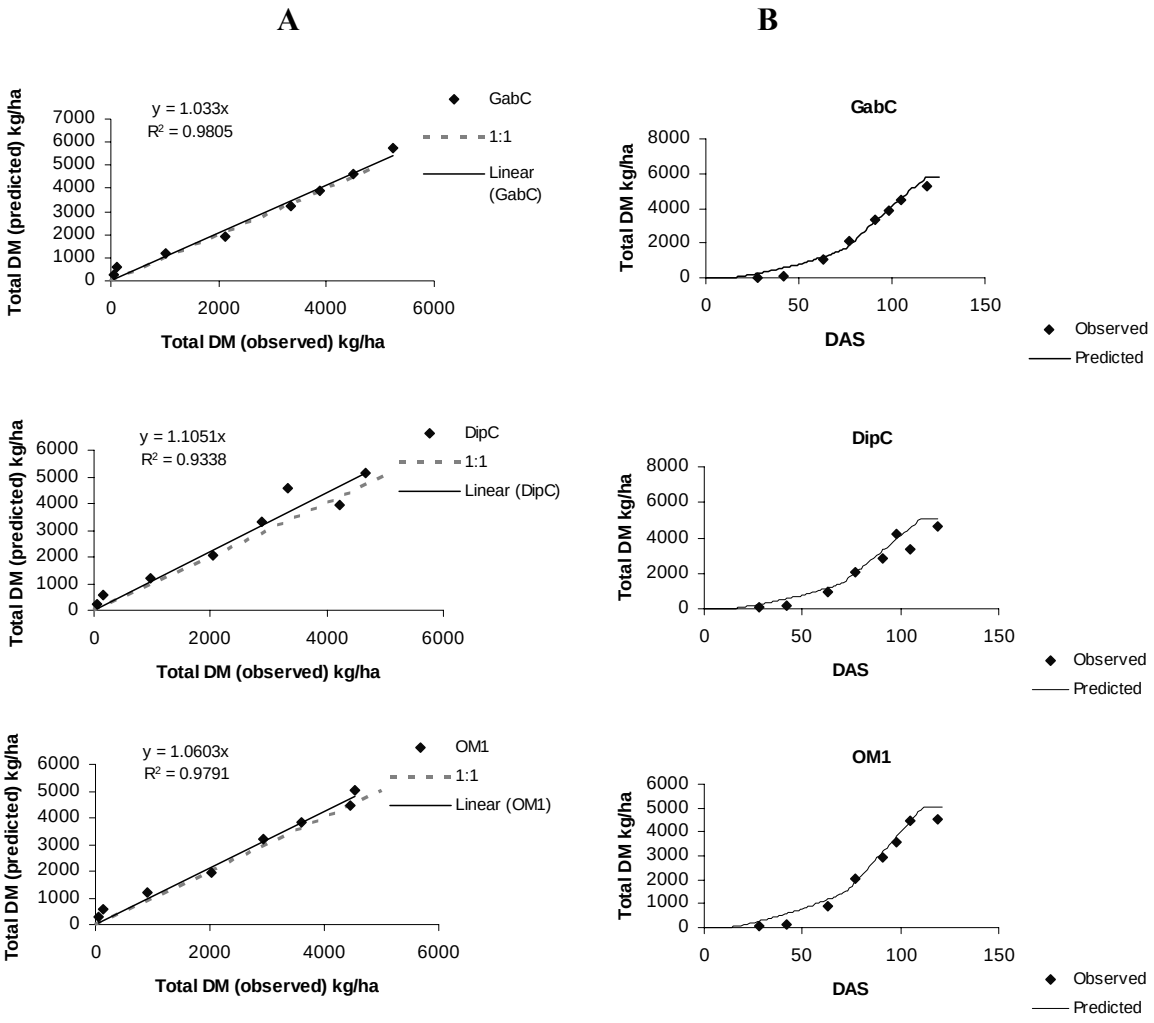

Figure 8-4: Relationship between observed and predicted total above ground biomass (Total DM kg ha^{-1}) (A) and the relationship between observed and predicted above ground biomass (Total DM kg ha^{-1}) with time (Days After Sowing, DAS) for Botswana landraces (GabC, DipC and OM1) (B) at Malkerns.

The model achieves an excellent fit between observed and predicted total above ground biomass for all Botswana landraces (Figure 8-4).

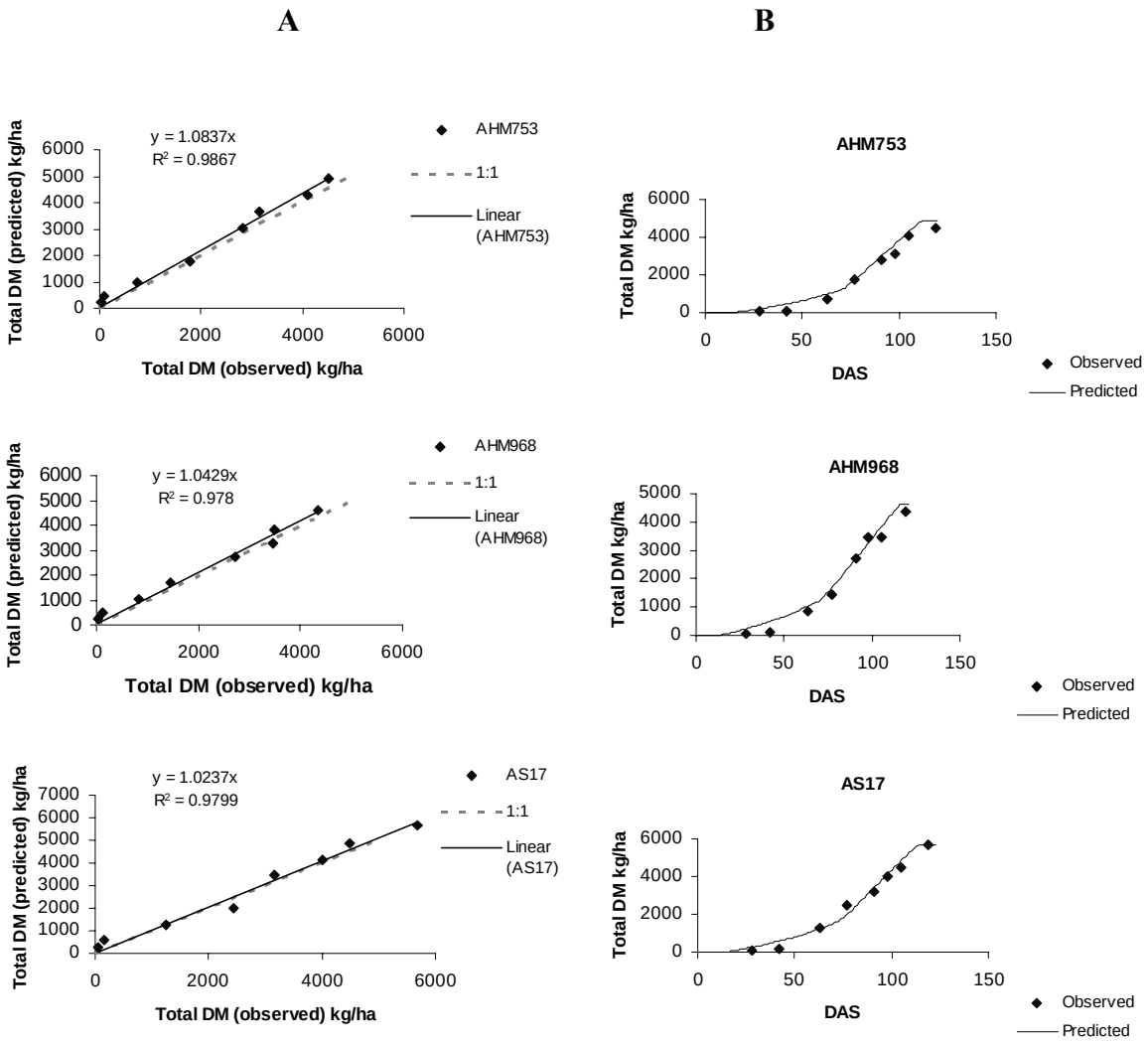

Figure 8-5: Relationship between observed and predicted total above ground biomass (Total DM kg ha^{-1}) (A) and the relationship between observed and predicted above ground biomass (Total DM kg ha^{-1}) with time (Days After Sowing, DAS) for Namibia landraces (AHM753, AHM968 and AS17) (B) at Malkerns.

The model again achieves an excellent fit between observed and predicted total above ground biomass for all Namibian landraces (Figure 8-5).

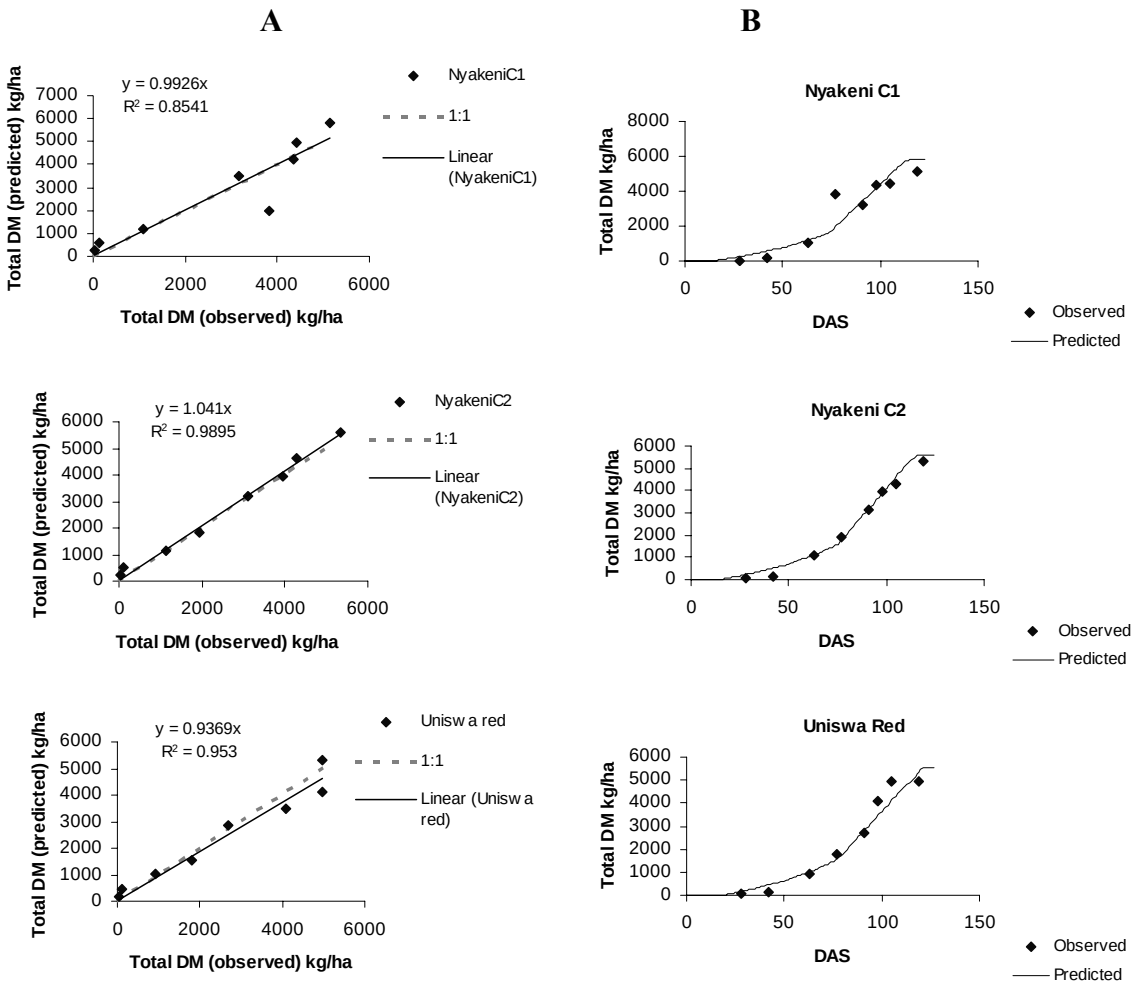

Figure 8-6: Relationship between observed and predicted total above ground biomass (Total DM kg ha^{-1}) (A) and the relationship between observed and predicted above ground biomass (Total DM kg ha^{-1}) in time (Days After Sowing, DAS) for Swaziland landraces (NyakeniC1, NyakeniC2 and Uniswa Red) (B) at Malkerns.

Overall, the model excellently predicts the total above ground biomass for all Swazi landraces (Figure 8-6)

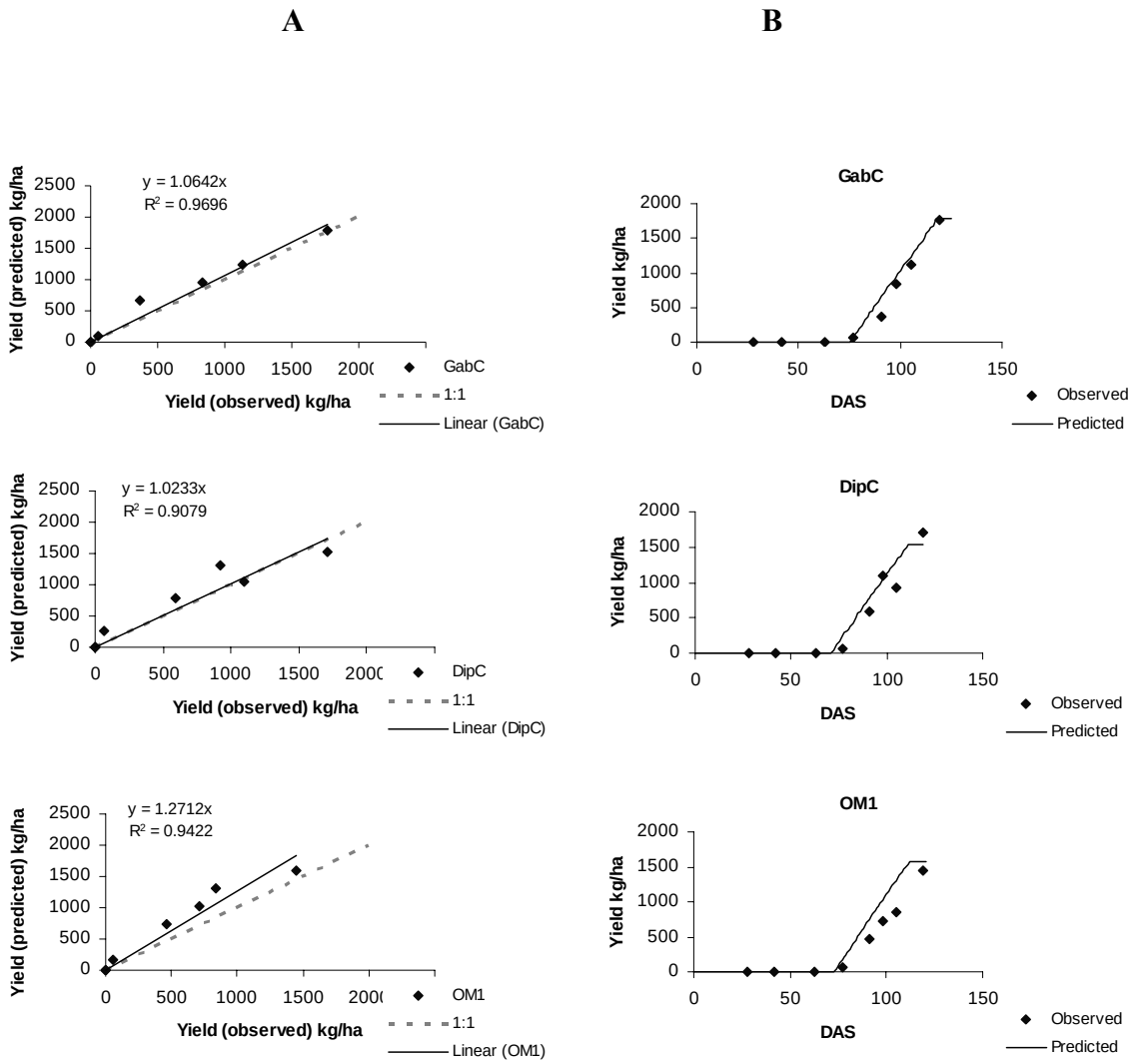

Figure 8-7: Relationship between observed and predicted pod yield (kg ha^{-1}) (A) and the relationship between observed and predicted pod yield (kg ha^{-1}) with time (Days After Sowing, DAS) for Botswana landraces (GabC, DipC and OM1) (B) at Malkerns.

All landraces have a very strong correlation between the observed and predicted pod yield. (Figure 8-7). The model shows an excellent prediction of pod yield for GabC and DipC but a slight overestimate for the pod yield of OM1.

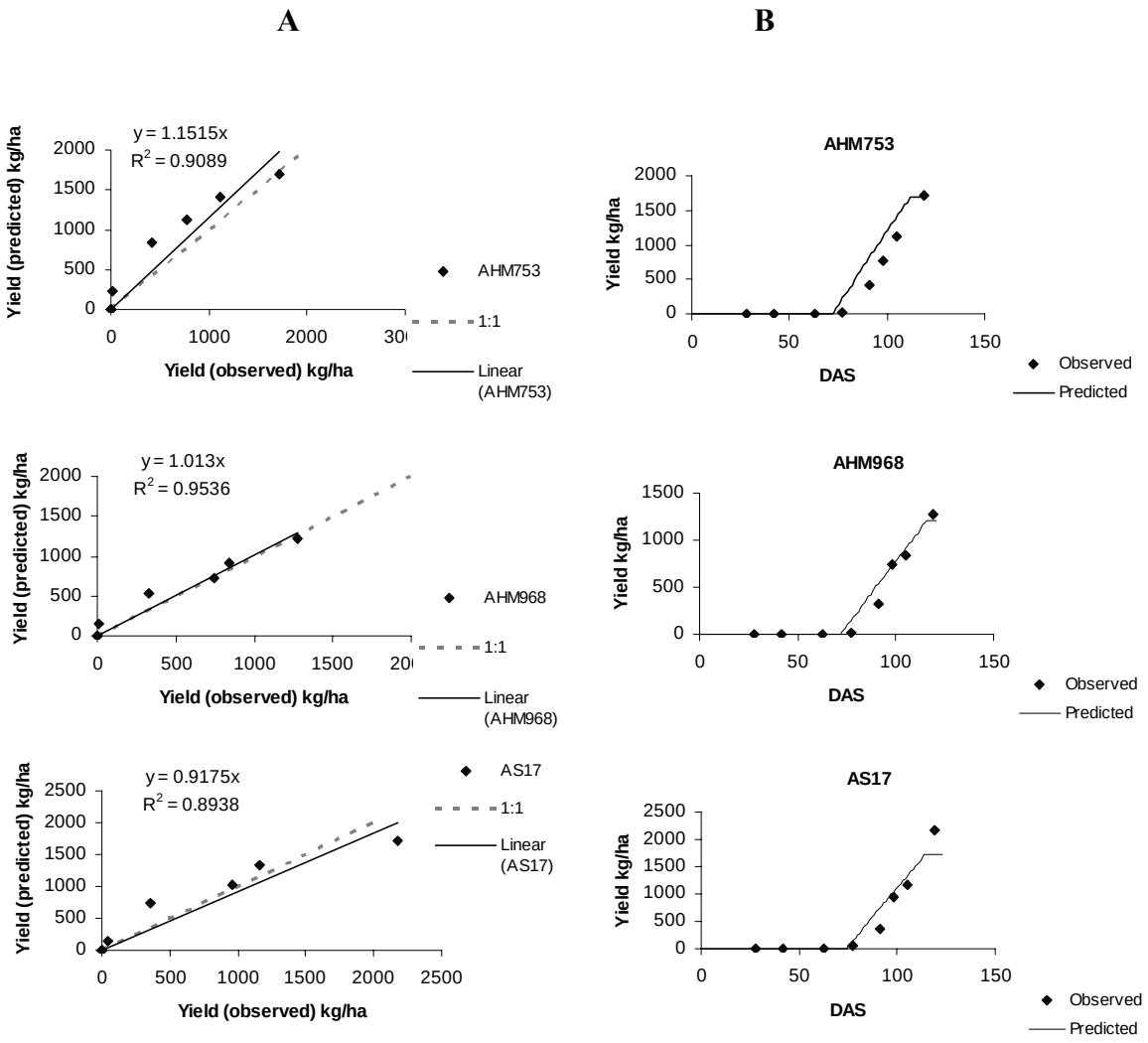

Figure 8-8: Relationship between observed and predicted pod yield (kg ha^{-1}) (A) and the relationship between observed and predicted pod yield (kg ha^{-1}) with time (Days After Sowing, DAS) for Namibian landraces (AHM753, AHM968 and AS17) (B) at Malkerns.

The correlation between the predicted and observed values of pod yield is very good for the Namibian landraces (Figure 8-8).

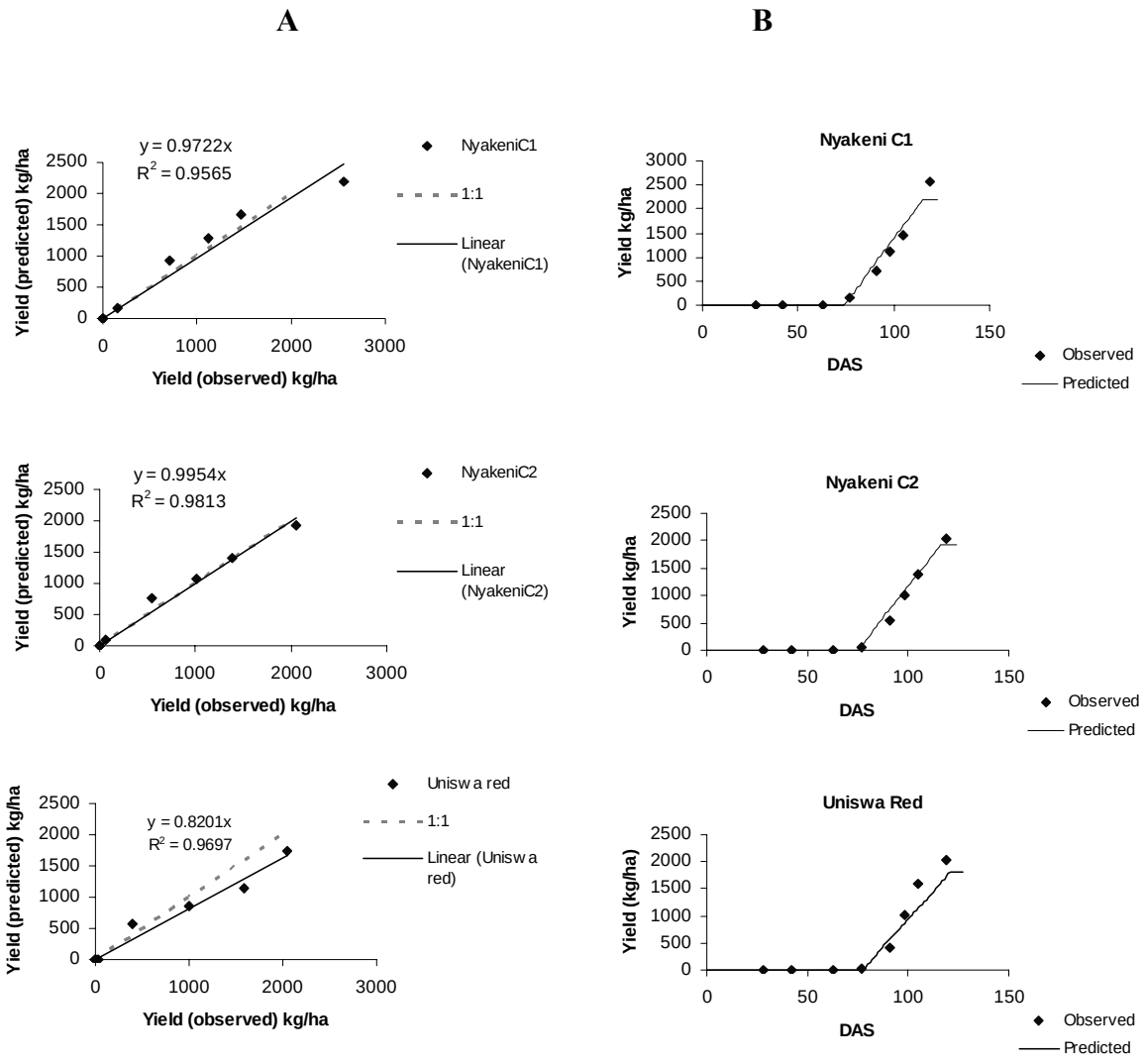

Figure 8-9: Relationship between observed and predicted pod yield (kg ha^{-1}) (A) and the relationship between observed and predicted pod yield (kg ha^{-1}) with time (Days After Sowing, DAS) for Swaziland landraces (NyakeniC1, NyakeniC2 and Uniswa Red) (B) at Malkerns.

Figure 8-9 shows that the model achieves a good fit between observed and predicted pod yields for NyakeniC1 and NyakeniC2. It slightly underestimates the pod yield of Uniswa Red. The correlation between the observed and predicted values of pod yield is excellent.

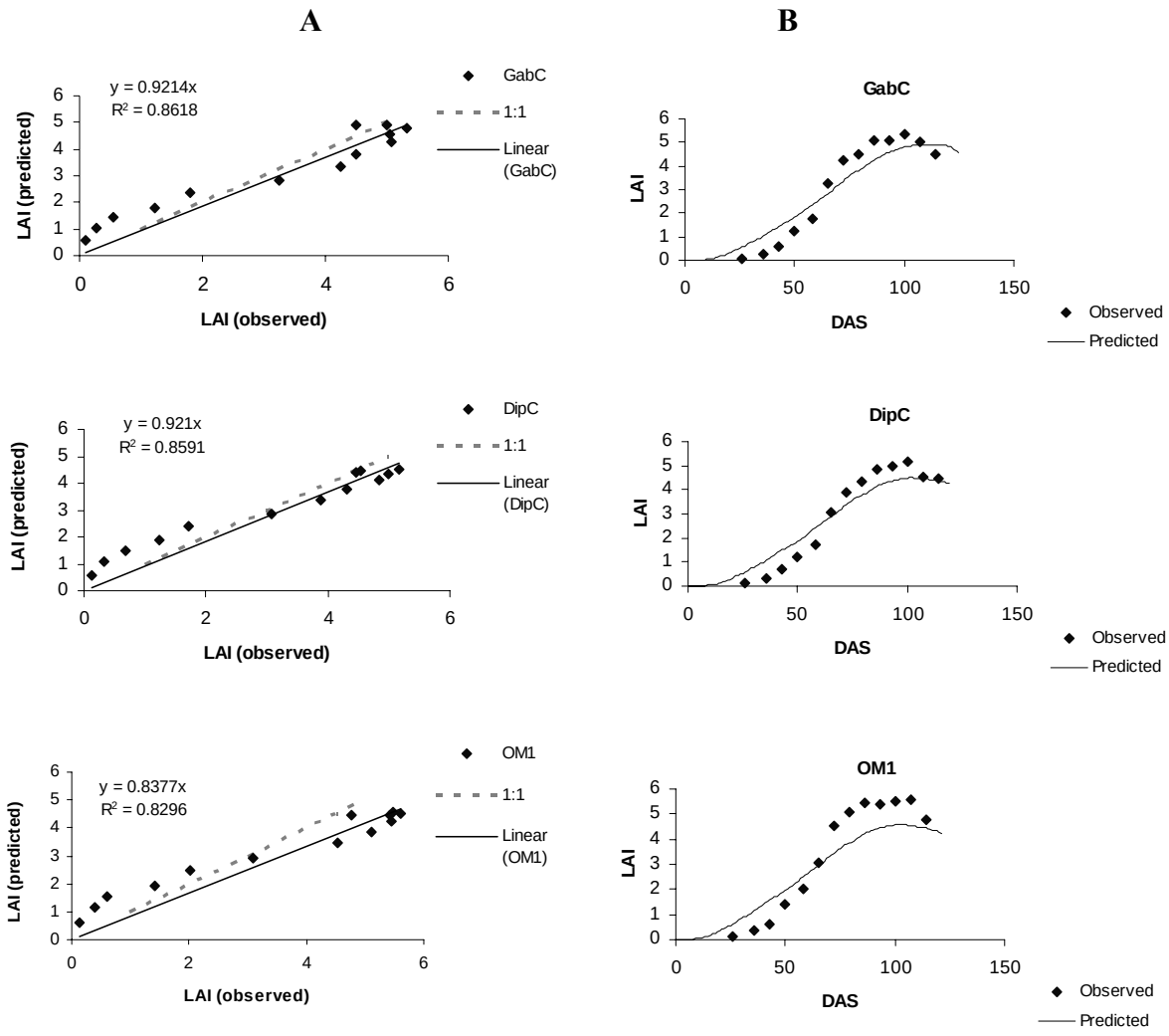

Figure 8-10: Relationship between observed and predicted Leaf Area Index (LAI) (A)and the relationship between observed and predicted LAI with time (Days After Sowing, DAS) for Botswana Landraces (GabC, DipC and OM1) (B) at Malkerns.

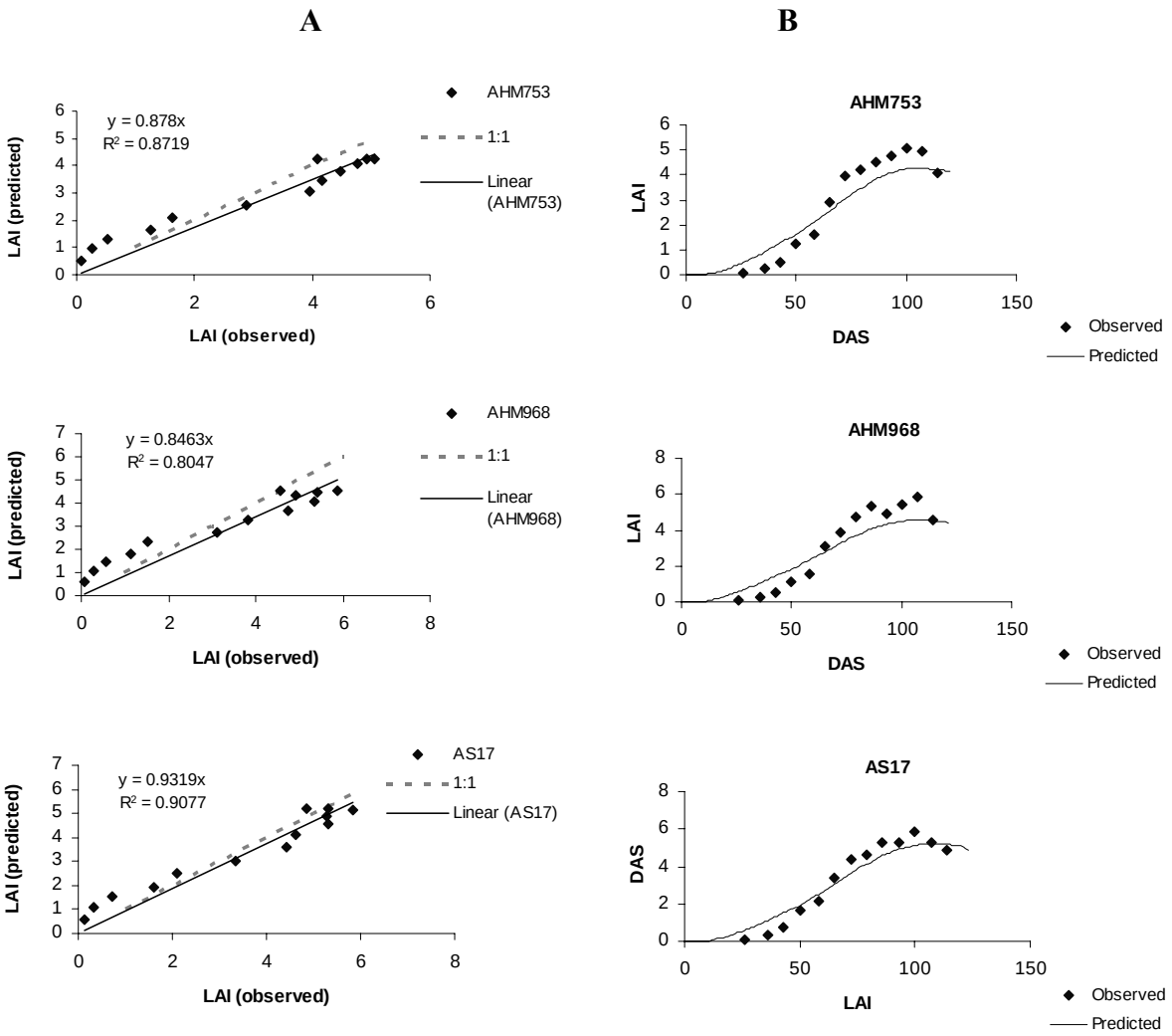

Figure 8-11: Relationship between observed and predicted Leaf Area Index (LAI) (A) and the relationship between observed and predicted LAI with time (Days After Sowing, DAS) for Namibia landraces (AHM753, AHM968 and AS17) (B) at Malkerns.

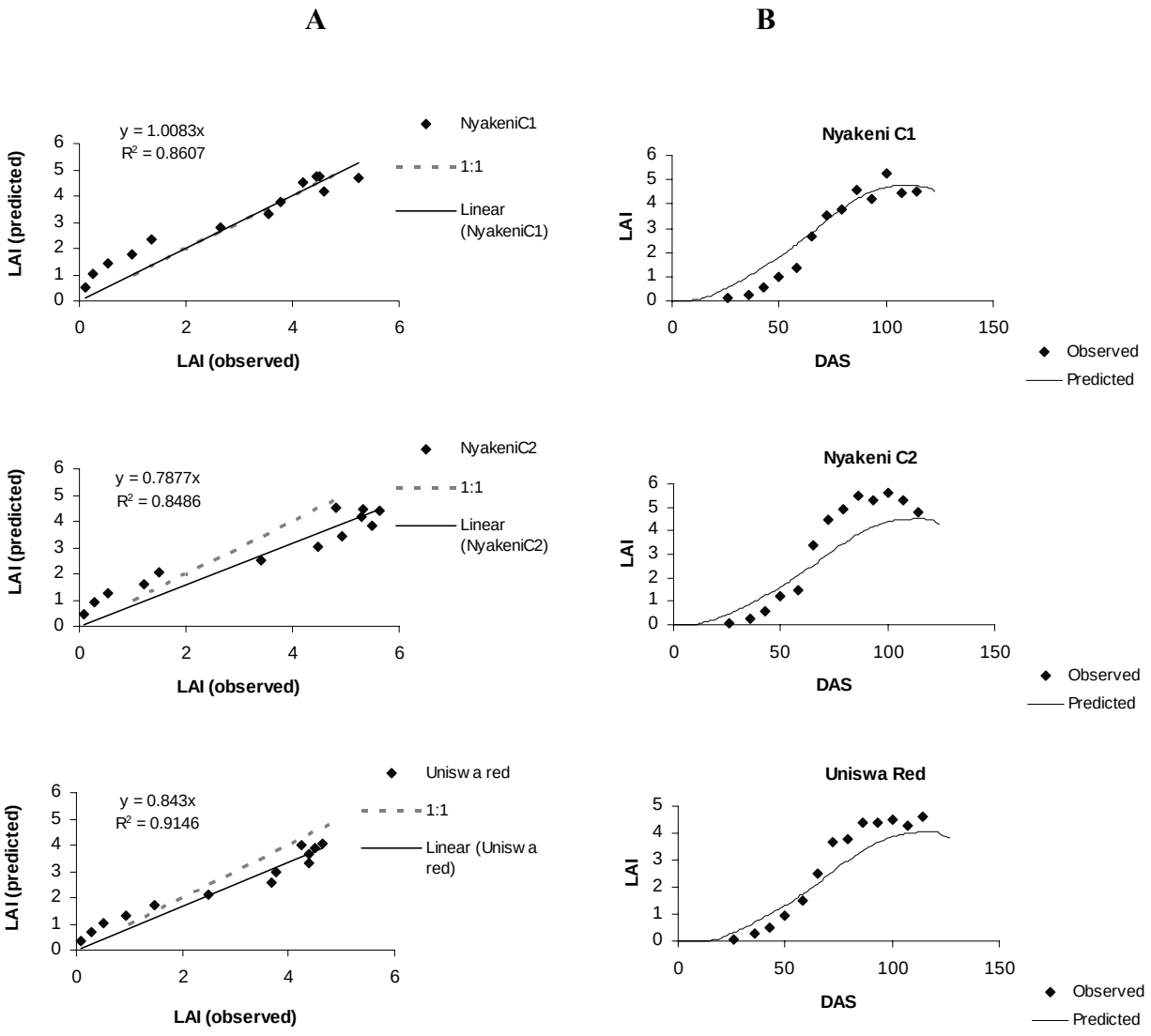

Figure 8-12: Relationship between observed and predicted Leaf Area Index (LAI) (A)and the relationship between observed and predicted LAI with time (Days After Sowing) for Swaziland landraces (NyakeniC1, NyakeniC2 and Uniswa Red) (B) at Malkerns.

Figure 8-10, Figure 8-11 and Figure 8-12 show that the model slightly underestimates the total LAI for all landraces in the field. However, the shape of the predicted curve is very similar to the observed values. The model seems to overestimate the LAI early in the season but the curve flattens at the end of the season. There exists a strong correlation between the observed and predicted values.

8.2.3 Luve field data

The Luve field data have been included to test the capability of the model to handle drought. Luve has a very coarse sandy soil, with a sand fraction of 80% (Sesay, 2003). After checking the rainfall before the simulation started (no rain fell for more then 10 d before planting), combined with the coarse, fast draining soil and high temperatures the initial soil water content has been assumed to be 0 m^3 H_2O m^{-3} soil in the top meter of the soil. This assumption was supported by a reported initial soil moisture content of 0.07 m^3 H_2O m^{-3} soil in 2002 (INCO-DC, Second annual report, 2002). Three landraces were tested, one from each country. These were: Uniswa Red (Swaziland), OM1 (Botswana) and AS17 (Namibia).

Figure 8-13 shows the model performance for predicting total above ground biomass in the Luve experiment.

A strong correlation exists between the predicted and observed total above ground biomass for all landraces. However the model underestimates the total above ground biomass for both Uniswa Red and OM1. For AS17, the model gives a good fit. In all cases the general shape of the predicted curve is very similar to the observed values.

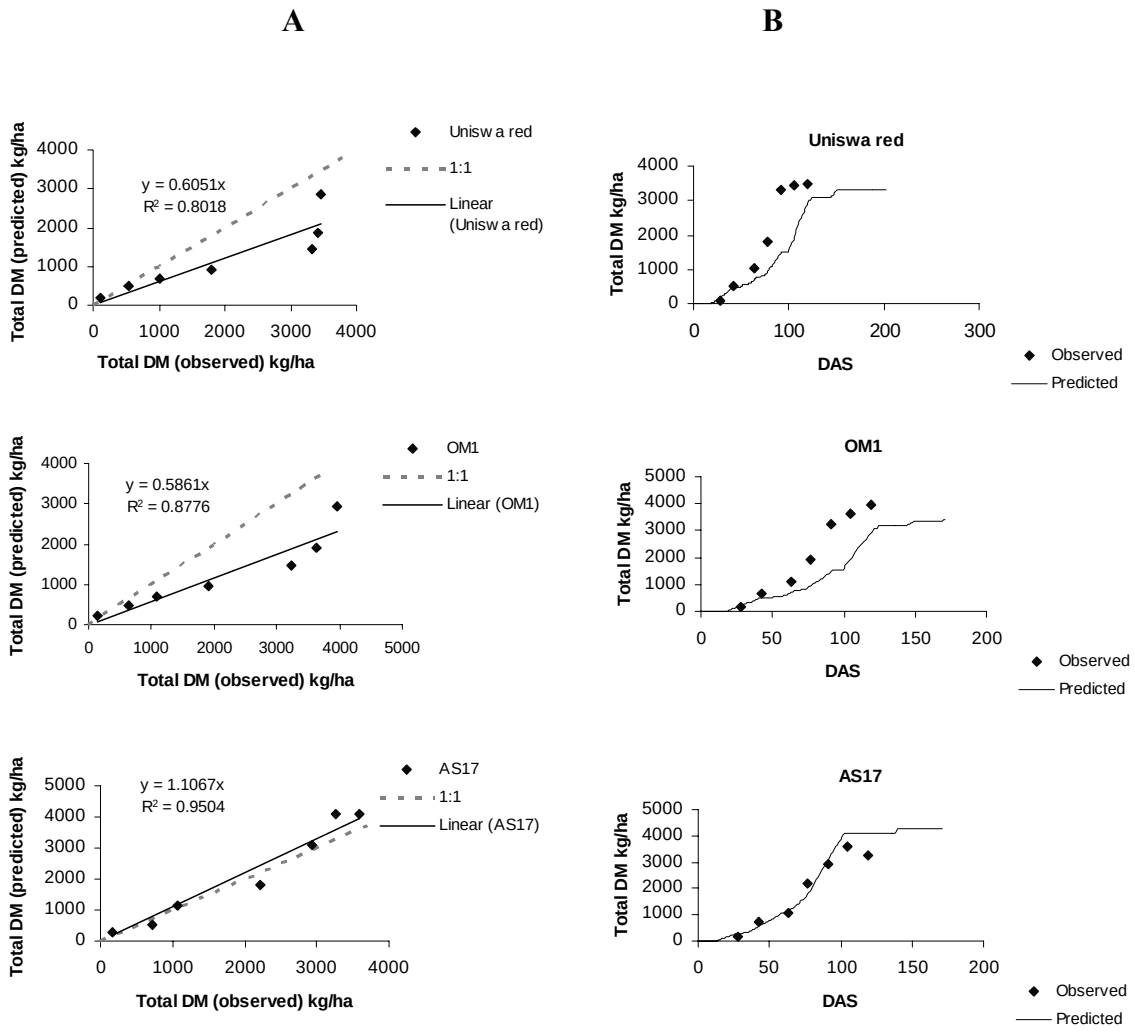

Figure 8-13: Relationship between observed and predicted total above ground biomass (Total DM kg ha^{-1}) (A) and the relationship between observed and predicted above ground biomass (Total DM kg/ha) with time (Days After Sowing, DAS) for Uniswa Red, OM1 and AS17 (B) at Luve.

A strong correlation exists between the predicted and observed total above ground biomass for all landraces. However the model underestimates the total above ground biomass for both Uniswa Red and OM1. For AS17, the model gives a good fit. In all cases the general shape of the predicted curve is very similar to the observed values.

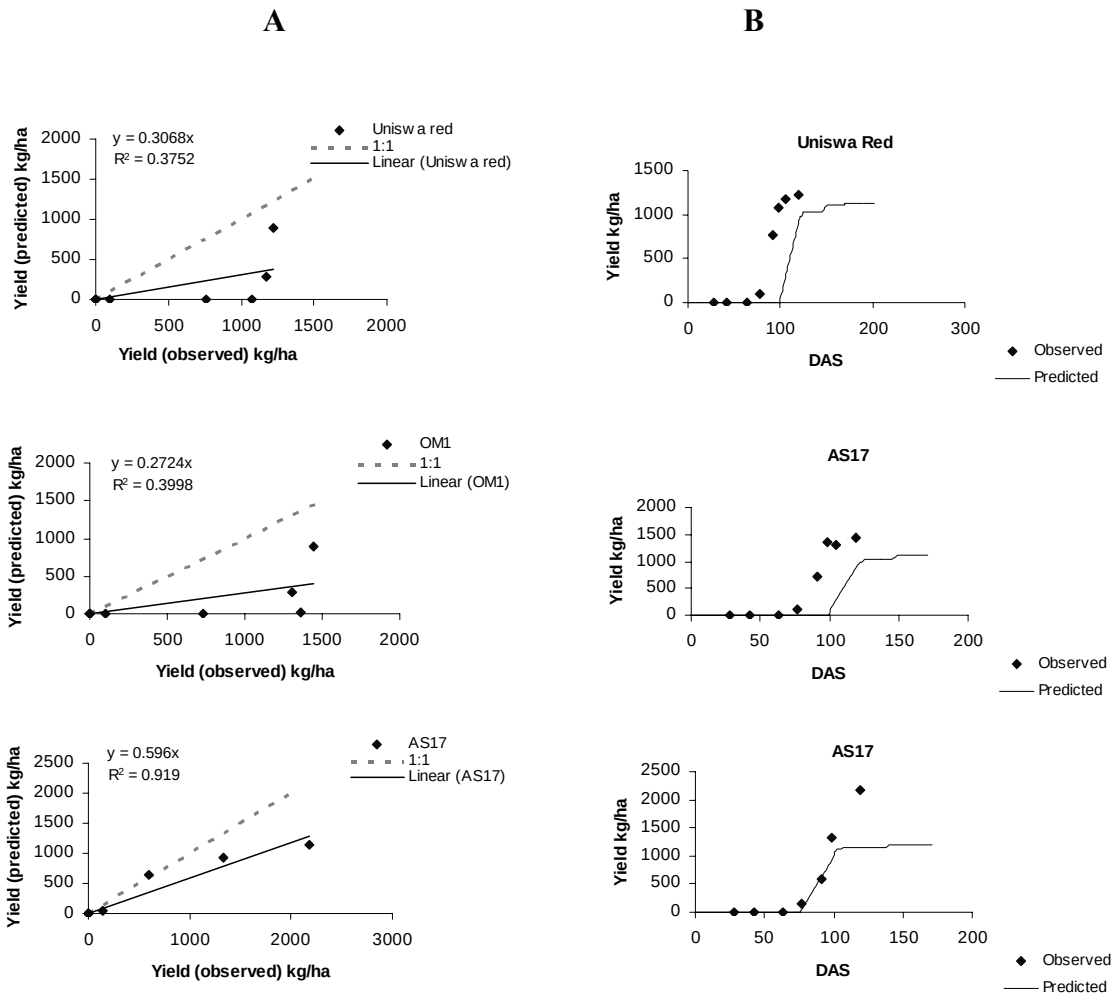

Figure 8-14: Relationship between observed and predicted pod yield (kg ha^{-1}) (A) and the relationship between predicted and observed pod yield (kg ha^{-1}) with time (Days After Sowing, DAS) for Uniswa Red, OM1 and AS17 (B) at Luve.

There is a strong correlation between observed and predicted pod yield for AS17, however the model considerably underestimates the yield as represented on Figure 8-14. There is no correlation between observed and predicted pod yield for Uniswa Red and OM1, however the shape of the fitted curve is similar to the observed values. It seems that the model predicts the start of pod filling to be later than that observed.

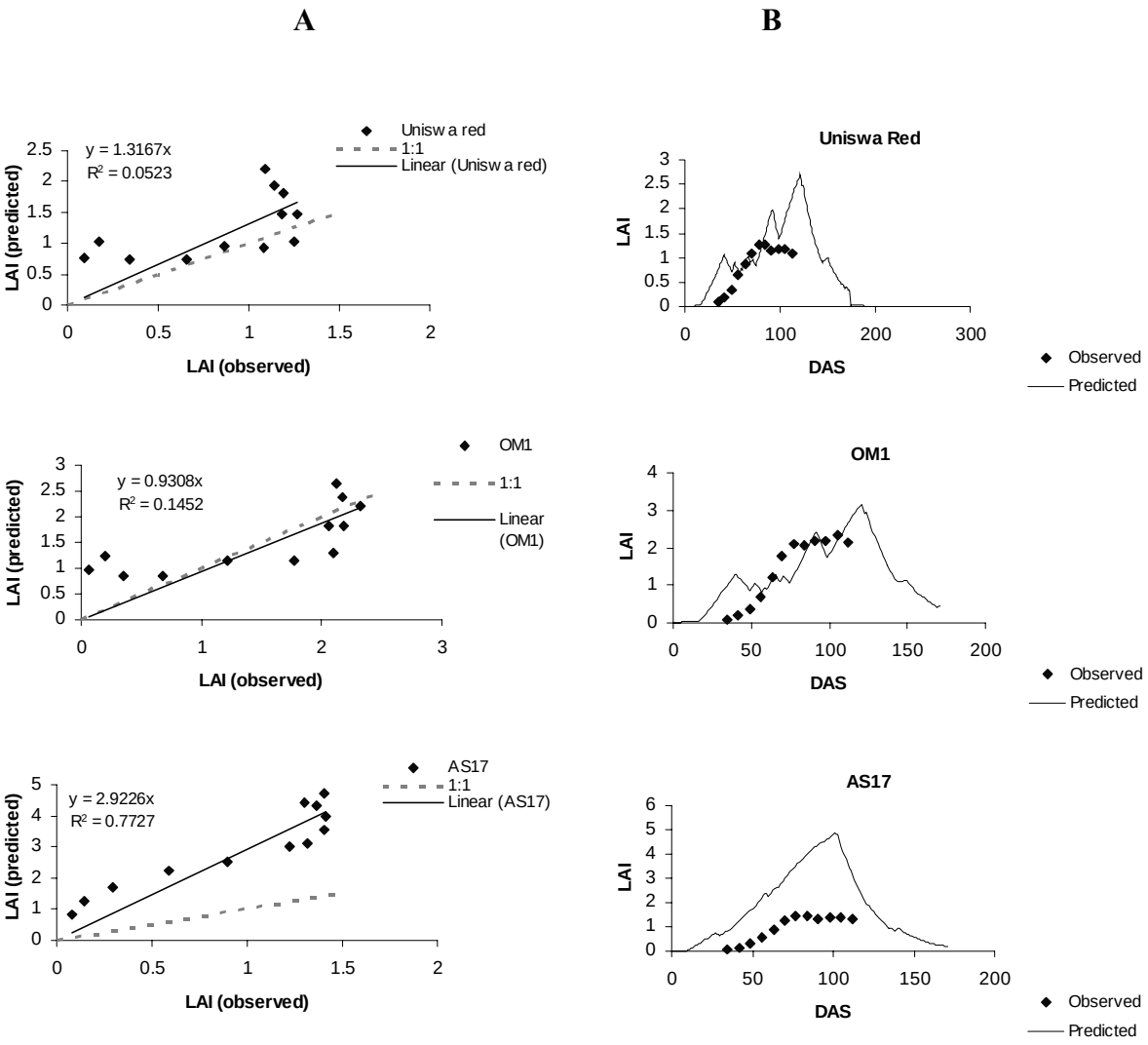

Figure 8-15: Relationship between observed and predicted Leaf Area Index (LAI) (A) and the relationship between predicted and observed LAI with time (Days After Sowing) for Namibian landraces (NyakeniC1, NyakeniC2 and Uniswa Red) (B) at Luve.

There is a correlation between observed and predicted LAI for AS17, however the model considerably overestimates the LAI (Figure 8-15). There is no correlation between observed and predicted LAI for Uniswa Red and OM1 and the model overestimates the LAI considerably. The LAI is gravely overestimated in the early stages of the crop for all three landraces. The LAI is calculated as a function of leaf number and the model is overestimating leaf production in the early stages, because it is not simulating the slowing effect of drought on leaf production.

Figure 8-13 to Figure 8-15 seem to show that the water routine does not handle water stress particularly well. The model seems to predict total above ground biomass reasonably well for two of the three landraces. Pod yield is underestimated for AS17 and is delayed for the other two landraces.

Table 8-2: Observed and predicted final pod yield and final total above ground biomass for Uniswa Red, OM1 and AS17 using data from the Luve field site, Swaziland.

Landrace	Pod yield (kg ha^{-1})		Total DM (kg ha^{-1})	
	Observed	Predicted	Observed	Predicted
Uniswa Red	1217	1120	3422	3331
OM1	1444	1129	3971	3407
AS17	2176	1206	3260	4272

The model can be seen in a slightly different perspective when the final total above ground biomass and final pod yield are looked at in more detail (Table 8-2). For Uniswa Red both the predicted values are within 10% of those observed. For OM1 the total above ground biomass and yield are still within 20 % of the observed. Only AS17, despite having the best fitting curves, is the furthest off the mark in both situations.

8.3 SENSITIVITY OF THE MODEL TO MAJOR INPUTS AND PARAMETERS

In order to determine the sensitivity of the model to changes in some of its major inputs and parameters the validated model has been run several times, only changing the input or parameter. The model has been run with GabC parameters and a Malkerns weather file. Initial soil moisture was 0.28 m^3 H_2O m^{-3} soil, unless stated otherwise.

The inputs were solar radiation, initial water content and total seasonal rainfall. The parameters were the phyllochron interval and the Specific Leaf Area. The effects of change have been shown for final pod yield and final total above ground biomass.

8.3.1 Solar Radiation

Solar radiation is an important input to the model as all biomass production is related to the possible growth rate, determined by solar radiation. In many tropical areas solar radiation is not measured directly but has to be estimated using the Ångström equation (Chapter 7). In order to test the influence of solar radiation on the predictions of the model, BamGro was run three times. Firstly with an unchanged weather file, then with an extra 10% solar radiation per day and finally 10% less solar radiation per day. The results can be seen in Table 8-3.

Table 8-3: Effect of a 10% change in solar radiation on final yield and final above ground biomass of bambara groundnut as predicted by the BamGro model.

		Yield ($kg\ ha^{-1}$)	Total DM ($kg\ ha^{-1}$)
Daily Solar Radiation	-10%	1774	5973
	0	1774	6055
	+10%	1774	6137

An increase or decrease of 10% of the daily solar radiation does not lead to any change in pod yield and only results in a 2% change in total above ground biomass.

8.3.2 Initial soil water content

The initial soil water content is an important factor determining if the crop is going to be drought stressed over the season. It is important to know for which soil type the model is running, as some soil types can lose water quicker then others. The model was run for a sandy loam soil with four different initial soil water contents, 0.12, 0.20, 0.28 and 0.36 $m^3\ H_2O\ m^{-3}$ soil. The results can be seen in Table 8-4.

Table 8-4: Effect of four initial soil water contents on final pod yield and final above ground biomass of bambara groundnut as predicted by the BamGro model

		Yield ($kg\ ha^{-1}$)	Total DM ($kg\ ha^{-1}$)
Initial Soil Water Content ($m^3\ H_2O\ m^{-3}$ soil)	0.12	1728	5952
	0.20	1778	6046
	0.28	1774	6055
	0.36	1774	6080

The sandy loam soil used for these runs of the model does not seem to be influenced by the initial soil water content. Tripling the initial water content only leads to a change of less than 5% in the final yield and total above ground biomass. The initial soil moisture does have an effect on the duration of the growth season. This explains the higher yield in the second run, as the crop went through a longer pod filling stage.

8.3.3 Total seasonal rainfall

Rainfall can be extremely variable in semi-arid Africa. It is important to know how the model responds to a change in total seasonal rainfall. The model was run for a sandy loam soil with an initial soil water content of 0.28 m^3 H2O m^{-3} soil. The results can be seen in Table 8-5.

Table 8-5: Effect of 100 mm change in total seasonal rainfall on final yield and final above ground biomass of bambara groundnut as predicted by the BamGro model.

		Yield ($kg\ ha^{-1}$)	Total DM ($kg\ ha^{-1}$)
Seasonal rainfall (mm)	369	1743	5927
	469	1774	6055
	569	1774	6084

The sandy loam soil used for these runs of the model does not seem to be influenced by the range of seasonal rainfall used in this analysis. A 21% decrease in total seasonal

rainfall only leads to a change of less than 2% in the final yield and total above ground biomass.

8.3.4 Phyllochron interval

The phyllochron interval is very important in the model. It not only determines the number of leaves but is directly linked to the prediction of the leaf area and the distribution of dry matter over the different plant components. Three runs have been completed for the model with a difference of 10% between the phyllochron intervals.

Table 8-6: Effect of a phyllochron interval on final pod yield and final above ground biomass of bambara groundnut as predicted by the BamGro model.

		Yield (kg ha^{-1})	Total DM (kg ha^{-1})
Phyllochron interval	0.29	1774	6689
(number of leaves $plant^{-1}$ $(phenochron)^{-1}$)	0.32	1774	6055
	0.35	1774	5558

As can be seen in Table 8-6 A 10% change in the phyllochron interval leads to a 10 % change in total above ground biomass. The phyllochron interval does not influence the yield.

8.3.5 Specific Leaf Area

The Specific Leaf Area is used in the model to predict the dry matter distribution over the crop components. The SLA seems to be very variable between landraces and even growing conditions. Three runs have been completed with an SLA of 225, 250 and 275 cm^2 g^{-1}.

Table 8-7: Effect of Specific Leaf Area on final yield and final above ground biomass of bambara groundnut as predicted by the BamGro model..

		Yield (kg ha^{-1})	Total DM (kg ha^{-1})
SLA	225	1732	6414
(cm^2 g^{-1})	250	1774	6055
	275	1774	5710

A 10% increase or decrease in SLA leads to a 5% change in total above ground biomass (Table 8-7). A decrease in SLA results in a small change in pod yield, but an increase in SLA does not affect the yield.

8.3.6 Pod weight increase constant

The pod weight (P_{con}) increase constant predicts the yield per plant in the model and is used to calculate the total yield and influences the way dry matter is distributed over the plant. The P_{con} seems to be very variable between landraces. Three runs have been completed with a P_{con} of 0.84, 0.93 and 1.02 g phenochron^{-1}. All but one of the tested landraces (AHM968 has a P_{con} of 0.62) fall within this range of P_{con}.

Table 8-8: Effect of pod weight increase constant on final yield and final above ground biomass of bambara groundnut as predicted by the BamGro model.

		Yield (kg ha^{-1})	Total DM (kg ha^{-1})
P_{con}	0.84	1603	5933
(g phenochron^{-1}.)	0.93	1774	6055
	1.02	1946	6177

A 10 % increase or decrease in P_{con} leads to a 10% change in pod yield as seen in Table 8-8. The total above ground biomass is less affected by a change in P_{con} (in the order of 1%).

8.4 DISCUSSION

8.4.1 Validation

BamGro accurately predicts the yield, total above ground biomass and LAI for the Malkerns field site in Swaziland, on which most of its parameters are based (i.e. it is a calibrated model for this site). In the TCRU glasshouses it accurately predicts the LAI. The total above ground biomass is under estimated in the glasshouse, this might be a consequence of the low values of solar radiation in the glasshouse compared to the field, combined with a change in the partioning between roots and above ground biomass in the glasshouse, compared to the field.

The predictions for the Luve field site are still poor. This is mostly the result of the fact that the water routines could not be validated, because water measurements in the field were not available.

8.4.2 Implications of the sensitivity of the model to major inputs and parameters

The sensitivity analysis revealed that the model is sensitive to the crop parameters used by BamGro. It is therefore important that these parameters are determined with great care. Bambara groundnut is an underutilized crop and available data are still limited. Furthermore the physiological response of bambara groundnut to environmental stress is not yet fully understood. Care must be taken when the model is used in an environment were it has not been tested.

The model seems to be not very sensitive to changes in seasonal rainfall and initial soil moisture content. The model was tested for a sandy loam, with a good water holding capacity. The difference in initial water content (0.12 – 0.36 m^3 H_2O m^{-3} soil) may not make a large difference in available water over the growth season. Furthermore the model was tested for the Malkerns field site in Swaziland. Rainfall distribution was

fairly even over the season, without prolonged period without any rainfall. A difference of 100 mm over the total growth season might not lead to a real water stress at any time. It can be expected that the model will be much more sensitive to total rainfall, when the rainfall is less evenly distributed and the crop experiences longer periods of drought.

CHAPTER 9 CASE STUDIES: EXAMPLES OF MODEL USE

In this chapter three examples of the BamGro model use will be presented. The first example will be the comparison of three different landraces in two different environments. Secondly, the use of the model to evaluate hypothetical plant material to aid a possible breeding program. Finally it will show long term yields of a landrace in an environment.

9.1 COMPARISON OF THREE LANDRACES IN NAMIBIA AND BOTSWANA

One of the uses of a crop model is to predict the biomass production and yield of a variety or landrace of a crop in an environment where it has not been grown before. Instead of actually growing a large range of varieties/landraces in a number of field sites and seasons, a well validated model combined with a set of landraces for which the necessary model parameters have been determined could be used to predict the behaviour of the varieties/landraces and the most suitable for specific locations can be chosen.

As an example, in this chapter three landraces, have been chosen (Table 9-1). Predictions for total above ground biomass and pod yield have been made using BamGro for Notwane, Botswana (latitude: 24°33′ S, longitude: 25°54′ E, altitude: 994 m a.s.l, annual rainfall: 400-600 mm) and Mahanene, Namibia (latitude: 17°27′ S, longitude: 14°45′ E, altitude: 1110 m a.s.l., annual rainfall: 400 mm).

Table 9-1: Three landraces used in this example

Landrace	Origin	Seed colour
GabC	Botswana	Cream
AHM968	Namibia	Tan
Nyakeni C2	Swaziland	Cream

The MarkSim (Jones and Thornton, 2000) weather generator was used to generate a season of weather data for both sites. It has been assumed that the crops are planted after the start of the rains and the soil is at field capacity. An initial soil moisture content of 0.28 m^3 H_2O m^{-3} soil has been used. The soil type was a sandy loam (saturation point: 0.40 m^3 H_2O m^{-3} soil, field capacity: 0.28 m^3 H_2O m^{-3} soil and permanent witlting point: 0.15 m^3 H_2O m^{-3} soil) which can be found throughout the region, with a sand fraction of 0.39 and silt fraction of 0.10. The model was run with four zones in the top 1 meter of the soil and the PALM (Matthews, 2005) water routines were used. At both sites the plants were sown on 12 December 2001. The results of the model can be seen in Table 9-2.

Table 9-2: Predicted yield and total above ground biomass for three landraces in Namibia and Botswana.

Landrace		Yield (kg ha^{-1})	Total above ground biomass (kg ha^{-1})
GabC	Namibia	1810	6052
	Botswana	717	3308
AHM968	Namibia	1220	4747
	Botswana	565	2780
Nyakeni C2	Namibia	1972	5888
	Botswana	844	3344

Table 9-2 clearly shows large differences in yield between the landraces and the different sites. In both cases Nyakeni C2 seems to be the best choice for the locations.

The values shown in Table 9-2 agree with those found in the literature for Botswana (Chui *et al*., 2003), but are higher than those reported in Namibia (Kaulihowa and Philander, 2002). MarkSim generated an annual rainfall of 472 mm which compares well with the mean annual rainfall of 400 mm reported for Mahanene (Kaulihowa and Philander, 2002). The assumption of the soil being at field capacity during sowing might have prevented the crop experiencing drought.

More important than knowing the prediction for one year yield is knowing the yield stability over more than one year, specially in a variable climate. The model was run for simulated weather data for 5 years using the same starting variables. The results are shown in Table 9-3.

Table 9-3: Predicted five year yield and total above ground biomass for three landraces in Namibia and Botswana (average ± standard error of the mean).

		Namibia		**Bostwana**	
Landrace	Year	Yield (kg ha^{-1})	Total above ground biomass (kg ha^{-1})	Yield (kg ha^{-1})	Total above ground biomass (kg ha^{-1})
GabC	1	1810	6052	717	3308
	2	1741	5717	275	2300
	3	1780	5894	242	2159
	4	1754	5794	0	1320
	5	1791	6055	1356	5022
	Average	**1775 ± 28**	**5902 ± 152**	**518 ± 535**	**2822 ± 1422**
AHM968	1	1220	4747	565	2780
	2	1206	4611	273	2009
	3	1221	4663	223	1835
	4	1206	4629	0	1115
	5	1233	4777	988	4041
	Average	**1217 ± 11**	**4685 ± 73**	**410 ± 381**	**2356 ± 1113**
Nyakeni C2	1	1972	5888	844	3344
	2	1956	5656	377	2402
	3	1932	5722	311	2185
	4	1912	5694	0	1268
	5	1909	5834	1570	5190
	Average	**1936 ± 27**	**5759 ± 98**	**620 ± 611**	**2872 ± 1477**

Table 9-3 clearly shows that although Nyakeni C2 seems to be the best choice for the locations, there is a large difference in the stability of the yields and above ground biomass production between the sites. The variation in yield and above ground biomass is very low in Namibia. Due to the very variable climate in Botswana, however, Bamgro predicts very low yields three out of five years, with complete crop failure for all landraces one out of five years.

9.2 COMPARISON OF AN IDEOTYPE WITH AN EXISTING LANDRACE IN SWAZILAND

An approach to develop new crop varieties is through breeding based on the use of crop ideotypes. Crop ideotypes are plants with model characteristics known to influence photosynthesis, growth and grain production (Donald, 1968). Donald argued that, as with the design of aircraft, buildings and instruments, the design and breeding of crop plants could be usefully centered on a theoretical model based on the knowledge, experience and imagination of agricultural scientists. Donald further stated that however crude this model might be, it provides a combination of characters that might otherwise not occur in breeder's plots for centuries.

Based on farmers surveys and consumer research in Swaziland, Botswana and Namibia (Sesay *et al.*, 2003a; Ramolemana *et al*., 2003; Magagula *et al*., 2002; Fleissner, 2002; Hampson *et al*., 2000), the following characteristics for a hypothetical bambara groundnut variety (an ideotype) are most important:

1. High yield for the conditions and specific environment
2. Cream seeded
3. Large plant
4. Early maturing (short growth cycle)

As an example, a hypothetical ideotype has been created, based on realistic assumptions of selective breeding and availability of traits in the existing germplasm. The model parameters for the ideotype were based on the existing parameters from the nine landraces used in this study. In order to test the new ideotype and compare it with an existing landrace (GabC), BamGro was run for both the existing landrace and the ideotype. The differences between GabC and ideotype can be seen in Table 9-4.

Table 9-4: Comparison of model parameters between an existing landrace (GabC) and an Ideotype.

	GabC	Ideotype
Phyllochron interval (no. leaves plant^{-1} (phenochron)$^{-1}$)	0.32	0.29
Specific Leaf Area (cm^2 g^{-1})	270	235
Length of vegetative stage (phenochrons)	25	23
Podding constant ($P_{con,}$ g phenochron^{-1} (plant)$^{-1}$)	0.93	1.07

BamGro was run with Malkerns weather data and an initial soil moisture content of 0.28 m^3 H_2O m^{-3} soil for both GabC and an Ideotype. The sowing date was 25 November 2001. The results of the run can be seen in Table 9-5.

Table 9-5: Comparison between an existing landrace (GabC) and an Ideotype.

	GabC	Ideotype
Pod yield (kg ha^{-1})	1774	1997
Total above ground Biomass (kg ha^{-1})	5774	6820
Days till full cover (LAI = 3)	68	63
Crop Cycle (days)	125	121

Table 9-5 shows that the ideotype would have a slightly higher yield, larger plant and shorter crop cycle. However, the advantages are not great, presumably because the existing landrace is already well suited to making use of likely environmental resources.

The difference between the ideotype and the existing landrace may seem comparatively small and the results of the simulation rather obvious, a shorter vegetative period, results in shorter crop duration and a faster pod weight increase, will lead to more pods. This is only an example and only four parameters were changed. However all these traits already exist in the gene pool and selection for these traits and breeding real varieties can become a reality in the near future.

This approach allows the collation of field and controlled environment data and linking of these data with farmer knowledge and preferences to guide breeding activities rather than respond to them.

More important than knowing the prediction for one year yield, is knowing the yield stability over more than one year, specially in a variable climate. The model was run for simulated weather data for 5 years using the same starting variables. The results are shown in Table 9-6.

Table 9-6: Five year comparison between an existing landrace (GabC) and an Ideotype (average ± standard error of the mean).

Landrace	Year	Pod yield (kg ha^{-1})	Total above ground Biomass (kg ha^{-1})	Days till full cover (LAI = 3)	Crop Cycle (days)
GabC	1	1746	6144	78	162
	2	1794	6116	96	336
	3	1772	6071	91	191
	4	1769	6119	82	167
	5	1763	6106	69	159
	Average	**1769 ± 17**	**6111 ± 26**	**83 ± 11**	**203 ± 75**
Ideotype	1	2036	7604	70	157
	2	2035	7525	84	214
	3	2026	7345	83	180
	4	2018	7430	75	160
	5	2010	7367	64	155
	Average	**2025 ± 11**	**7454 ± 109**	**75 ± 9**	**173 ± 25**

Table 9-6 clearly shows that the variation in yields, above ground biomass and days till full cover is very low. For both GabC and the Ideotype the duration of the cropcycle is longer in year 2 due to a cooler period during grainfilling.

In the longer term BamGro could provide a mechanism through which molecular characterization and genetic linkage mapping can be linked with end-users (through the use of ideotypes). One important outcome of the BAMFOOD project is the development of the first ever genetic linkage map of the species (Basu *et al*., 2003).

Traits identified in this genetic approach provide powerfull tools that can be used in selection programmes, for example in terms of resource use, plant habit and seed colour.

9.3 FIFTEEN YEAR YIELD PREDICTION OF GABC IN SWAZILAND

The uncertainty in crop yield related to weather and other biophysical factors associated with particular management strategies can be quantified through repeated simulation using a crop model (Bannayan and Crout, 1999). Semenov and Porter (1995) proposed linking a weather generator to a crop model to provide real time simulation of crop growth and assessment of crop productivity.

Long term predictions or crop forecasting can give a good insight into the stability of yields and the chance of crop failure, especially in an environment with a variable climate. The decision-making capacity of farmers and resource planners would be greatly improved if they had some means in quantifying risk associated with particular strategies (Bannayan and Crout, 1999). Crop forecasting can provide an important tool for agricultural planning in both developed and developing countries (Stephens and Middleton, 2002).

To illustrate the crop forecasting ability of BamGro, the yield of GabC in Swaziland has been predicted for a period of fifteen years. MarkSim (Jones and Thornton, 2000) was used to generate fifteen weather data files for Malkerns, Swaziland and the model has been run for these fifteen years. The initial soil moisture for each run was 0.28 m^3 H_2O m^{-3}soil and the sowing date was 25 November. In this example, yield is only dependent on the variability of the climate.

Table 9-7 clearly illustrates the potential use of a crop model combined with a weather generator for crop forecasting. As a result of climatic variability the yields vary from 1196 to 1779 kg ha^{-1}. Table 9-7 also clearly shows that the yields seem to remain very stable over the years, with a yield of over 1730 kg ha^{-1} in thirteen out of fifteen years and no complete crop failure even in the lowest rainfall year (611 mm in Year 9).

Table 9-7: Fifteen year yield predictions for GabC in Swaziland

Year	Pod yield (kg ha^{-1})	Total Seasonal Rainfall (mm)
1	1765	763
2	1594	825
3	1196	615
4	1779	1366
5	1770	670
6	1778	829
7	1771	925
8	1762	1556
9	1746	611
10	1735	853
11	1772	794
12	1769	905
13	1763	1075
14	1738	1115
15	1769	960
Average (± standard error of the mean)	**1714** ± **150**	**924** ± **265**

The predicted yield for year two is lower than the other years because a long period without rainfall occurred in the middle of the growing season, resulting in a drought stress for the crop. The results of these predictions agree with those found in the literature (Sesay *et al*., 2003b; Sesay *et al*., 2002).

CHAPTER 10 SYNTHESIS

10.1 WHAT IS NEW ABOUT BAMGRO?

BamGro aims to account for differences between landraces in terms of growth, development and yield, and is mainly based on field experiments in Swaziland. The model is then adapted to predict growth, development and yield of the same landraces across a range of glasshouse environments. Landrace specific parameters have been derived from germplasm that has been taken from field locations in Namibia (annual rainfall = 400 – 600 mm), Botswana (annual rainfall = 400 – 500 mm) and Swaziland (annual rainfall = 700 – 1000 mm).

BamGro is the first model of bambara groundnut that attempts to use a simplified approach of simulating the effects of photoperiod on pod initiation and it attempts to incorporate water as a limiting factor. BamGro has been validated against independent data sets both in the field and the glasshouse. Although these routines could not be thoroughly tested and validated, due to the unavailability of soil water and photoperiod data, the inclusion of the routines is a major improvement on the previous models.

BamGro has been developed with clear end uses in mind. It is reasonably able to predict the performance of a given landrace in its own environment or in an environment in which it has not yet been grown. In this way the model can help to identify an appropriate landrace for a specific environment.

A second important feature of BamGro is that by incorporating local knowledge and farmers preferences as defined in the BAMFOOD project, regional ideotypes can be developed. BamGro allows the design of virtual “varieties”, which are based on the existing physiological potential of specific landraces and traits within the species (as seen in Chapter 9).

10.2 LIMITATIONS AND FUTURE DEVELOPMENT OF THE BAMGRO MODEL

10.2.1 Photoperiod sensitivity

It is well known that photoperiod sensitivity ranges in landraces from photoperiod insensitive to sensitive for both flowering and pod formation (Linnemann, 1991).

BamGro uses a simplified approach to take the photoperiod into account, which is the same for each landrace and thus ignores any differences that might exist between the landraces. However preliminary observations in the glasshouse (pot experiment 2001, see Chapter 3) and a field experiment in July 2001 at Sutton Bonington campus, UK (not described in this thesis), were photoperiod was not controlled, showed that the landraces (Uniswa Red, S19-3, DipC and AS17) all flowered as normal, but did not form pods. It was thus decided that BamGro only affects the pod formation. BamGro will prevent pod initiation in seasons with long days.

A first step in improving the photoperiod simulation in the model would be the determination of the delay of pod initiation due to photoperiod of each landrace in this study by growing the landraces under controlled photoperiod regimes. The existing photoperiod routine will then be able to distinguish between landraces.

Alternatively, Brink (1997) modelled the influence of photoperiod and temperature on the rate of progresss from sowing to flowering to podding of three bambara groundnut landraces, according to the photothermal approach developed at the University of Reading (Summerfield *et* al., 1991; Hadley *et al*., 1984). This model uses one to three linear equations to relate the rate of progress to flowering to photoperiod and/or temperature (Brink, 1997). This approach is then repeated for the rate from sowing to podding. In the most complex situation (rates are dependent on both temperature and photoperiod) the model needs six landrace dependent parameters.

A research priority could be the establishing the parameter values for the landraces used in this study and incorporate the model of Brink (1997) in BamGro. This should significantly improve the simulation of photoperiod, and landraces that are sensitive to photoperiod for both flowering and podding can be incorporated.

10.2.2 Drought

One of the major limitations during the development of the model was the unavailability of data on the water status of the soil. Neither initial water content, nor water content of the soil over the season was measured in the field. The initial water content of the soil and the water release characteristics of the soil, during the simulations were assumptions.

Observed changes in growth, production and yield could not be linked to a quantified water stress in the field. Attempts were made to study water use in the TCRU glasshouses (Mwale, 2003), however limited data exist on water status and water use of the landraces. Furthermore the experiments used in this project in the TCRU glasshouses only allow a comparison between a wet and a dry treatment. In order to test the model over a range of different moisture conditions, growing landraces under a range of moisture regimes would be desirable.

The BamGro model currently uses the PALM water (Matthews, 2005) routines which reduce growth and leaf area expansion. This agrees with literature (Mwale *et al*., 2003; Collinson *et* al., 1999; Collinson *et al*., 1996). Phenology, however, is unaffected by drought in BamGro.

There is evidence in the literature however that phenology might be affected by moisture stress. Collinson *et al*. (1999) report that bambara groundnut flowers longer, indicating a delay in the pod filling phase, similar to what can be observed in the response to photoperiod. The factors that control, flowering and pod filling may or may not be different for each landrace and the physiological bases for these differences are not yet understood.

Only limited physiological data on plant water status is available. More research is needed to develop a better understanding of how the crop responds to seasonal drought and determine which parameters of BamGro will be affected.

Quantifying the response of bambara groundnut to drought, especially the response of phenology should be a research priority. A similar routine, as the routine for photoperiod could be added to the model when the data becomes available.

10.2.3 Nitrogen response and nitrogen fixation

In its present state, BamGro does not take nitrogen into account and assumes the nitrogen to be a non limiting factor. Although there has been a recent interest in the response of bambara groundnut to nitrogen and other major nutrients (Edje *et al*., 2002), there is not a lot of data available on the subject.

Nitrogen response (and response to other major nutrients) could be modelled in a similar way as the response to soil moisture. Based on the ratio between nitrogen uptake and supply, a multiplier can be calculated which adjusts the growth of the plant, when a critical level is reached. A similar approach has been used in other modeling efforts (e.g. Robertson *et al*. 2001).

Nitrogen levels in the soil, nitrogen transformations and movement through the soil have been modeled extensively for other modeling efforts (e.g. Probert *et al*. 1998) and a similar model could be incorporated in BamGro.

Bambara groundnut is a legume and, like most legumes is capable in fixing nitrogen (Uguru and Ezeh, 1997; Kishinevsky *et al*., 1996; Gueye and Bordeleau,1988). Further more it has been reported that bambara groundnut can fix nitrogen in the presence of NO_3 in the soil (Dakora, 1998), making it a perfect crop to grow in intercropping systems, were inorganic fertilizer is applied.

A great asset to the BamGro model would be a routine describing the nitrogen fixation by the nodules. As still very little is known about the nodulation and capability of bambara groundnut to fix nitrogen, this should be quantified first. Kumar Rao and Dart (1987) showed a correlation between nodule number and crop size in pigeon pea (*Cajanus cajan*). If a similar relation exists for bambara groundnut the potential nodulation could be modelled using the approach of Sinclair (1986), were the potential daily rate of nitrogen fixation is a function of crop biomass, discounted for soil water stress.

More research is required into the interaction between nitrogen fixation by the nodules and inorganic nitrogen. If bambara groundnut is indeed capable of fixing nitrogen in addition to a response to inorganic nitrogen, the model somehow needs to model the combined effect of both sources.

10.2.4 Canopy shape and photosynthesis

The BamGro model uses an empirical equation to calculate drymatter production (Monteith, 1994). This model assumes light travels through the crop following Beer's law (Azam-Ali and Squire, 2002), assuming that the leaves are randomly distributed in the canopy.

Bambara groundnut has a sphere shaped canopy and field observations show a leaf arrangement that avoids shading of leaves, ensuring all leaves are optimally intercepting solar radiation. A problem encountered during model development was the underestimation of total above ground drymatter in the glasshouse. This might be a result of underestimating the photosynthetic potential of the plant, due to the special arrangement of the leaves.

A first step in testing this hypothesis would be trying to upscale the leaf measurements to the whole canopy, taking the photosynthesis of every leaf into account and comparing this with the estimation of total drymatter. If these significantly differ, a way of modeling the shape of the canopy should be found.

Matthews et al. (1988) describe radiation interception of a row of groundnut (*Arachis hypogeae*) by treating the canopy as half a cylinder and relating this to its interception. The canopy of a bambara ground could be modelled in a similar way.

10.3 UPTAKE OF THE MODEL

A major problem in the development of many models ensuring the uptake of the models after their development, especially in development countries.

Stephens and Hess (1996), in evaluating the uptake of the PARCH model in research institutions in Kenya, Malawi, Zimbabwe and Botswana, indentified a number of constraints to its uptake, which they classified as intellectual, technical and operational (Table 10-1).

Table 10-1: Constraints to the uptake of crop models (Stephens and Hess, 1996)

Intellectual constraints	No relevant application
	Not convinced of application
	Not convinced of credibility
Technical constraints	Haven't got the disk
	No access to computer
	Couldn't understand the program
Operational constraints	Couldn't obtain meteorological data
	Couldn't calibrate locally used cultivars
	Lack of technical support
	Lack of intellectual support
	Didn't believe results

Matthews *et al*. (2000) in addition report:

- Lack of validation of the models for local conditions.
- Difficulties in parameterising the models for local conditions.
- The models were sometimes unnecessary complex.
- Documentation was often poor.
- The models did not provide the answers being asked.

Furthermore, surveys of Decision Support Systems reported by Greer *et al.* (1995) suggest that the complexity of the user interface is one of the most limiting factors in their uptake. Other authors (Newman *et al.*, 2000; Knight, 1997) agree that a clear and easy to use interface is important.

In the development of BamGro, in the context of the BAMFOOD project, it has been attempted to address the above mentioned constraint. BamGro aims to model the growth and development of bambara groundnut as simply as possible, using only proven physiological relations, or relations that were based on actual measurements on the landraces used in the project. Unknown or poorly quantified relations, like photoperiod and drought have been incorporated in the model using simplified routines, which can be easily updated when sufficient quality data becomes available.

An attempt has been made to validate the model over different environments (glasshouse and field), but it is recognized that a further improvement of the water routine and consequently validation in extreme environments is required.

A major advantage of the BamGro approach was using the MarkSim weather generator (Jones and Thornton, 2000) for the generation of reliable weather data for use in Sub-Sahara Africa. The BamGro model is less dependent on climate data that is often difficult to obtain.

BamGro aims to model traits of bambara groundnut landraces that have been identified as being important by surveys of growers and consumers in the countries for which it was developed (Magagula *et al*., 2002; Edje *et al*., 2002; Manthe *et al*., 2002; Fleissner

et al., 2002). A difficulty of this approach is that many of the traits that come forward in these studies are qualitative (taste, seed colour, cooking time).

In the BAMFOOD project it was suggested to combine a landrace database which contains information on these qualitative traits with the BamGro model. The database can be searched for a desired trait or traits and will identify a landrace or group of landraces, which meet the criteria (Cornelissen, *et al*., 2003) and subsequently be run with BamGro to identify its agronomic potential.

An example of a user friendly interface has been presented on the International Bambara Groundnut Symposium, Botswana College of agriculture, Botswana, 8-12 August 2003. This interface could be linked to both the BamGro model and the above mentioned database, combining both into one easy to use software package. After improving the scientific part of the model, linking the interface to the model should be a major priority to insure a successful uptake of the model.

10.4 PREDICTING THE EFFECTS OF CLIMATE CHANGE

The balance of evidence now suggests that there is a discernable human influence on global climate (IPCC, 1996). While many of man's activities are involved, agriculture is an important one, both because of the influence it has on the emission of greenhouse gasses into the atmosphere, and also because of the impact that a changed climate is likely to have on agricultural production and its ability to meet the demands of the expanding population (Matthews *et al*., 2000).

The use of crop simulation models is one way in which knowledge on the influence of increased temperature and CO_2 can be extrapolated, not only outwards to a region but also forward in time and probably presents the best method we have at present of evaluating the likely effect of climate change (Matthews *et al*., 1997).

Unlike most staples many underutilized and neglected crops (like bambara groundnut) are adapted to various marginal growing conditions (Hammer *et al*., 2001). These crops

might be able to better cope with a harsher climate in the future. Having robust models of underutilized crops (like BamGro) enables the prediction of future productivity of these crops.

10.5 DOES BAMGRO WORK?

BamGro has been validated against independent data sets. It describes the basic physiology of growth and dry matter production of bambara groundnut very well for the non extreme environments in which it was developed, primarily in Swaziland. BamGro is capable of describing differences between landraces. However, the influence of both drought and photoperiod are already simulated using a simplified approach, and these aspects can be improved when sufficient high quality data becomes available.

Despite the limited evidence from field sites, the predictions of yield with BamGro outside the environments it has been validated in still fall within the range reported in the literature (Sesay *et al.*, 2002; Kaulihowa and Philander, 2002; Linnemann and Azam-Ali, 1993)

In summary BamGro is a basic and robust working platform which can be improved when more data becomes available.

10.6 CONCLUSIONS OF THIS STUDY

In Chapter 1.3 the objectives to this study were set out. A consice summary of how this study met these objectives is given here:

1. Identify the most important differences between bambara groundnut landraces. This study showed that there was no significant difference in the photosynthetic potential of the landraces. Pod number, i. e. the availibility of sinks, seemed to be the most important factor determining the yield.

2. Develop a suitable model framework. Based on this most important difference between landraces a model framework was developed. Simplified approaches to simulate both the effects of photoperiod and drought were also developed.
3. Develop landrace specific relations to calculate development and yield in bambara groundnut and built the model. The model (BamGro) is an adaptation of the PALM (Matthews, 2005) model for a leguminous crop. It is a sink-orientated model, i.e. the number of available sinks (pods) determines the final production. Landrace specific relations have been developed based on TCRU glasshouse data and Swaziland filed data.
4. Validate the model predictions against field and glasshouse data. BamGro has been validated against three independent sets of data. It describes the basic physiology of growth and dry matter production of bambara groundnut for the non extreme environments in which it was developed. BamGro is not yet capable to predict the growth and drymatter production under drought accurately.
5. Test the model outside the environment of development. BamGro has not been extensively tested outside the environment of development. However three examples of how Bamgro could be used have been presented.

10.7 RECOMMENDATIONS FOR FUTURE RESEARCH

Building a crop model always leads to the discovery of many gaps in the knowledge about the crop, as can be seen above this study was not different. The following list showes the most important gaps in knowledge that need to be addressed:

1. The study showed large differences in the leaf appearance rate and consequently leaf area expansion. Allthough there were indications that this was due to environment, probably a combination of higher plant densities in the glasshouse and radiation guality/quantity, this is not yet fully understood. More experiments to determine the effect of high plant density are required. Quantifying the effect of light quantity, i. e. growing the crop under different light regimes could be very usefull.

2. As described in §10.2 photoperiod has not yet been quantified for the landraces in this experiment. As photoperiod differences can have large implications on the production of bambara groundnut, it is of utmost importance that this is done for as many landraces as possible. At least the boundaries of the photoperiod sensitive period for both flowering and podding need to be quantified.
3. The effect of drought is not yet fully understood. Mwale (2005) compared an irrigated treatment with a droughted treatment and the effect of drought on the growth and development in the TCRU glasshouses. Mwale (2005) linked his findings to physiological measurement of the water status of the crop. He also studied root growth and distribution. Allthough this is a good start, only an irrigated and droughted treatment are compared. Future research should focus on trying to quantify the effect of different water regimes on the growth and development of bambara groundnut.
4. There has been a recent interest in the response of bambara groundnut to nitrogen and other major nutrients (Edje *et al*., 2002), but there is not a lot of data available on the subject. As bambara groundnut is a legume, it has the ability to fix nitrogen. The interaction between the response to added nitrogen and the own ability to fix nitrogen can be very important.
5. Recently a start of a molecular linkage map of bambara groundnut has been esthablished, linking genetics to physiological traits of agronomic interest (Basu *et al*., 2003). An interesting future development would be trying to link BamGro to this linkage map. BamGro can then be used not only to predict the growth and development of existing landraces, but could be used to predict the growth and development of possible varieties, based on these traits and genetic possibility.

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